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THE UNIVERSITY OF ALBERTA

Perspectives on Autecology and Population Biology of Alpine Cushion Plants

by

Ahmad Kamel Hegazy

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF Doctor of Philosophy
IN
Plant Ecology

Botany

EDMONTON, ALBERTA
Spring 1987

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THE UNIVERSITY OF ALBERTA

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled **Perspectives on Autecology and Population Biology of Alpine Cushion Plants** submitted by Ahmad Kamel Hegazy in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Plant Ecology.

Walter Moser

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External Examiner

Date 87-04-21

Abstract

Cushion plants are perennial chamaephytes with crowns attached to the soil surface. The six species investigated: *Eriogonum androsaceum* Benth., *Potentilla uniflora* Ledeb., *Saxifraga caespitosa* L., *Saxifraga bronchialis* L., *Silene acaulis* L., and *Dryas octopetala* L. show different distributions (lee/windward and wide/narrow range) in the alpine belt of Mount Allan, Alberta, Canada. Phenology, rooting characteristics, seed germination, CO_2 gas exchange, resource allocation, and water relations were examined. (1) Timing of phenological events differed more between species, than within the species at different sites. Buds, formed during the previous growing season, allow fast sprouting in spring. (2) Rooting patterns are site dependent. On steep slopes they are one-sided and extend in up-slope direction. Standing dead litter is a major part of the aboveground phytomass. The dead/live shoot ratios ranged from 1.01 to 3.72. (3) The seeds of the different species differ in their ability to germinate and to establish seedlings. Only *Saxifraga caespitosa* seeds did not germinate. (4) The net photosynthesis rates are low when compared to other alpine plants. The minimum and maximum compensation points were around 3°C and 35°C, respectively. The light compensation points ranged from 80 to 270μmol.m^{-2}.sec^{-1}. The saturation points ranged from 250 to

$650 \mu mol.m^{-2}.sec^{-1}$. Optimum temperatures were between 21 and 25°C. Respiration rates were relatively high (Range from 1.03 to 13.44 mg $CO_2.g^{-1}DW.\ h^{-1}$). (5) Based on site characters and resource allocation, both "pioneer" (e.g. *Eriogonum androsaceum* and *Potentilla uniflora*) and "climax" plants (e.g. *Dryas octopetala*) allocated more dry matter to vegetative than to sexual reproduction. (6) In spite of relatively high transpiration rates and high water saturation deficits, the plants were able to maintain high average water content. Water relations and anatomical features of the leaves indicate that the investigated species are xerophytes. (7) Generally, in contrast to the restricted species (e.g. *Saxifraga caespitosa*), the local widely distributed species (e.g. *Potentilla uniflora*) were characterized by: a) well developed root systems. b) high seed germination values. c) higher light compensation and saturation points but lower temperature minima and optima for photosynthesis. d) very low dry matter allocation to sexual reproduction. e) higher rates of transpiration and low water potentials.

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Table of Contents

Chapter Page

I. General Introduction 1

A. Cushion Plants 1

Definition 1

General Form 2

Global Distribution 4

B. Autecology and Population Biology 5

Objectives 6

Hypotheses 8

C. The Study Area 8

Location 8

Geology 10

Soil 11

Climate 12

Vegetation 15

D. Study Species 18

E. Summary 22

Bibliography 24

II. Species Distribution and Cushion Plant Cover Structure 28

A. Introduction 28

B. Methods 29

C. Results 30

Soil Moisture 30

Wind 32

Temperature 34

Vegetation 36

D. Discussion 44

E. Summary 45

Bibliography 46

III. Phenology 49

A. Introduction 49

B. Material and Methods 51

C. Results 55

D. Discussion 66

E. Summary and Conclusions 69

Bibliography 71

IV. Rooting Patterns 74

A. Introduction 74

B. Materials and Methods 76

C. Results 78

Root Morphology 78

Root/Shoot Ratios 86

Litter Accumulation 86

D. Discussion 89

E. Summary and Conclusions 97

Bibliography 99

V. Seed Germination Characteristics and Young Seedling Growth 103

A. Introduction 103

B. Material and Methods 105

Temperature 108

Light 108

Stratification 109

Seed Washing and Drying 109

Water Availability 109

Growth Regulators 110

Chilling and Drought Tolerance 111

C. Results 112

Response to Temperature and Light 112

Response to Stratification 119

Response to Washing and Drying 123

Response to Water Availability 125

Response to Growth Regulators 128

Seedling Response to Chilling and Dehydration 135

D. Discussion 137

Temperature and Light 137

Stratification 140

Seed Washing and Drying 141

Water Availability 142

Growth Regulators 145

Seedling Response to Chilling and Dehydration 149

E. Conclusions 151

F. Summary 153

Bibliography 155

VI. Carbon Dioxide Gas Exchange 162

A. Introduction 162

B. Materials and Methods 164

Carbon Dioxide Gas Exchange 164

Leaf Area Index (LAI) 170

C. Results 171

Effect of Temperature 171

Effect of Light 176

Leaf Area Index 180

D. Discussion 182

E. Species Distribution 190

F. Summary 191

Bibliography 193

VII. Resource Allocation 198

A. Introduction 198

B. Material and Methods 200

C. Results 201

Phytomass Distribution 201

Reproductive Allocation 204

D. Discussion 206

E. Summary 210

Bibliography 212

VIII. Water Relations and Leaf Anatomy 216

A. Introduction 216

B. Materials and Methods 219

Water Content 220

Transpiration 221

Water Saturation Deficit 221

Water Potential 222

Drying-out Curves 222

Water Loss from Cut Shoots 223

Anatomical Investigations 223

C. Results 225

Water Content 225
Transpiration 229
Water Saturation Deficit 232
Water Potential 235
Leaf Temperature 239
Drying-out Curves 242
Water Loss from Cut Shoots 247
Anatomical Measurements 249
D. Discussion 255
Water Relations 255
Ecological Significance of Leaf Anatomy ...262
Species Distribution 267
E. Conclusions 268
F. Summary 269
Bibliography 272
IX. General Discussion 280
A. Conclusions 280
Hypothesis 1 280
Hypothesis 2 281
Hypothesis 3 281
Hypothesis 4 282
Hypothesis 5 282
Hypothesis 6 283
B. Summary 284
X. Appendix 286

List of Tables

Table (2.1)	Cushion plant species distribution along three line transects down-up slope direction in different sites of the study area.	38
Table (2.2)	Presence and number of individuals, and presence and percentage cover data in 15 releves at various sites of the study area.	40
Table (3.1)	Characteristics of study area sites.	53
Table (3.2)	Phenological phases and their corresponding base scores.	53
Table (3.3)	The range of variability (absolute lowest and highest values) in phenological indices of the investigated species at the various study sites during the growing season of 1984.	57
Table (3.4)	The range of variability in numbers of flowering stalks produced per individual plant at various sites during the growing season of 1984.	64
Table (3.5)	Percentage of individuals per species population which failed to produce flowers during the growing season of 1984.	65
Table (4.1)	Root and shoot characteristics of the studied species at various sites of the study area.	87
Table (5.1)	Seed germination and seedling growth response of the different species to four growth regulators.	146
Table (6.1)	Leaf area indices of different leaf area classes of the six species at various sites of the study area.	181
Table (6.2)	Photosynthetic characteristics of the six species studied.	184

Table (7.1)	The average percentage of live dry matter components in the different species at various sites of the study area.	203
Table (7.2)	The average percentage of vegetative reproductive allocation (VRA) and sexual reproductive allocation (SRA) of the studied species.	205
Table (8.1)	Percentage water content at saturation, water content at the beginning and completion of stomatal closure, and rates of water loss with stomata shut.	246
Table (8.2)	Initial percentage water content, and the percentage of initial fresh weight and water losses over 24 hours.	248
Table (8.3)	Anatomical features of the leaves of the investigated cushion plants.	251

List of Figures

Figure (1.1)	The study area and site location on Mount Allan.	9
Figure (1.2)	Climate diagrams of two stations.	14
Figure (1.3)	Distribution of the investigated species in Alberta.	19
Figure (2.1)	Soil moisture content in the different sites of the study area.	31
Figure (2.2)	Daily course of wind velocity.	33
Figure (2.3)	Daily course of soil, cushion plant and air temperatures.	35
Figure (2.4)	The distribution of cushion plants along the elevation gradient on Mt. Allan.	42
Figure (3.1)	Plant phenological index of the studied species at various sites.	56
Figure (3.2)	Number of green leaves and dying-back leaves per branch of the studied species at various sites.	61
Figure (3.3)	Number of flowering stalks produced per individual plant of species studied at various sites.	63
Figure (4.1)	Root system sketches of species studied at various sites of the study area.	83
Figure (4.2)	Hypothetical model of one-sided root configuration.	92
Figure (5.1)	Effect of temperature and light and their interaction on seed germination of different species.	115
Figure (5.2)	Effect of stratification time on seed germination of different species.	122
Figure (5.3)	Effect of washing and drying of seeds on seed germination of different species.	124

Figure (5.4)	Effect of water stress (Osmotic pressure) and substrate water content on seed germination of *Potentilla uniflora* and *Silene acaulis*.	127
Figure (5.5)	Effect of four growth regulators on seed germination of different species.	131
Figure (5.6)	Effect of chilling and dehydration on seedling survival and establishment of *Potentilla uniflora, Silene acaulis* and *Saxifraga bronchialis*.	136
Figure (6.1)	Diagram of the IRGA system.	166
Figure (6.2)	Effect of leaf temperature (°C) on net photosynthesis and dark respiration of different species.	173
Figure (6.3)	Effect of light intensity on net photosynthesis of different species.	178
Figure (8.1)	Water content of transpiring organs at different air temperatures and water treatments.	227
Figure (8.2)	Transpiration rates at different air temperatures and water treatments.	231
Figure (8.3)	Water saturation deficit of the transpiring organs at different air temperatures and water treatments.	234
Figure (8.4)	Water potentials of the transpiring organs at different temperatures and water treatments.	237
Figure (8.5)	Leaf and air temperatures at different water treatments.	241
Figure (8.6)	Drying-out curves and stomatal aperture of detached transpiring shoots.	244

List of Plates

Plate (1.1) General view of Mt. Allan and vegetation ripples of cushion plants. 17

Plate (1.2) The study species. 21

I. General Introduction

A. Cushion Plants

Definition

According to Schimper (1903), Hauri(1912), Rauh(1939) and Krivonogova (1960), cushion plants are classified as:

1. Dense plants - with compact structure containing the "packing material", which includes a great variety of substances such as old leaves and twigs of the plant itself, and inorganic matter varying from fine particles to fairly large stones, overgrown or brought in by wind, rain, melting snow, etc. The internal living parts are practically excluded from light and sheltered from wind. That is, the plant produces a closed crown surface. Only a thin exposed layer of active leaves of the current season at the cushion surface is green.
2. Loose plants - when the spaces between the branches of the shoots are filled with more inorganic than organic substrate.
3. Aerial plants - when air pockets are found between the branches of the shoot. These cushions are penetrable by light, have no packing material, and are of a less compact structure.

According to Hauri and Schroeter (1914), there are about 377 cushion forming flowering plants from 34 families.

General Form

Cushion plants are perennial chamaephytes, forming rounded spherical, hemispherical or convex canopies closely attached to the soil surface. The shoot is formed by many rosettes, and each rosette consists of a number of green leaves. Dead leaves are not shed, but remain on the shoot, becoming part of the packing material and eventually being decomposed within the cushion.

The size of the plants varies greatly with age. In certain species of *Androsace* and *Saxifraga*, they scarcely exceed the size of moss cushions of *Grimmia* and *Barbula* (Schimper 1903), i.e., few cm in diameter. Others resemble masses of a coral, as in the case of the great cushions formed by certain Andean and Antarctic species of *Azorella*, *Laretia* and *Raoulia* which attain a height of two meters and even larger diameters (Ralph 1978, Alliende and Hoffmann 1983).

The age of cushion plants is not readily determined. However, Ralph (1978) concluded that at the low growth rate of cushion plants, many plants in the tropical Andes would be about 850 years old, and occasional individuals could be as old as 3000 years. A general feature common to dense and loose cushion plants is the accumulation of dead plant organs, particularly the leaves, on the shoot branches, which persist and contribute to the structure of the plant. Because of this feature, fresh plant nutrients are continually being released *in situ* by the decomposition of the dead organic matter. These nutrients are recycled by the same individual plant and used for further growth.

Energy is not the main limiting factor on cushion plant sites; the availability of nutrients is. Therefore, this recycling of nutrients gives cushion plants an advantage (Addison 1977, and Svoboda 1977).

Also, cushion plants are somewhat less exposed to nightly frosts than other alpine plants, due to the insulating cylinders of dry leaves around the stem. But since most of the stem is dead material in any case, this merely rises the question of how the plant's exposed living parts (leaves, buds, flowers) are protected from frost.

There can be no doubt that the cushion growth form of high mountain plants represents largely modifications induced by extreme environmental conditions (Schimper 1903, Warming 1909, Rauh 1939, and Hedberg 1964). The profuseness of branching is brought about largely by the growing tips being killed and growth being continued by lateral buds, though often other factors also play a role (Hauri 1913, Rauh 1939, and Smith 1972). As reviewed by Hedberg(1964), the cushion habit may result from strong winds, strong light (especially blue and ultraviolet light), low temperature, and lack of water. However, some studies have shown that high mountain cushion plants retain their stunted growth under ameliorated environmental conditions (Rauh 1939), that is, the habit appears to be genetically fixed.

Global Distribution

Cushion plants are widely distributed on the globe. They are commonly associated with the high mountains of all parts of the world, especially at the altitude of the alpine belt. Also, they are commonly found in arctic and subantarctic areas, and in cold and warm deserts. The majority of cushion plants is found in South America, namely in the Andes, Patagonia, and the Falkland Islands, and also in New Zealand (Krivonogova 1960). About 25 percent of cushion plants are recorded in the Himalayas and in the highlands of Asia (Hauri and Schroeter 1914). They are also prominent in the Alps and the highlands of Europe. In the Rocky Mountains of North America they are widely represented. The number of cushion plants occurring in the Afro-alpine flora is small compared to South America (Hedberg 1964), but a large number of cushion plants exists in the Sahara desert (Hauri 1912). Cushion plants are rare in the Antarctic (Huntley 1971).

In contrast to the northern hemisphere, the paucity of cushion plants in the Afro-alpine flora, as compared with the flora of the same latitude in South America, is very striking (Rauh 1939, Hodge 1946, and Hedberg 1964). Because of the present climatic parallelism between the two areas, the reasons for this difference seem evidently historical. The Andes also seem to have provided a convenient pathway for the dispersal of mountain plants, whereas the African mountains appear to have stood isolated from each other since their origin (Hedberg 1961).

B. Autecology and Population Biology

In recent years, there has been growing consensus that in order to increase our understanding of plant ecological phenomena, the coordination of autecological studies with population biology deserves priority (Mooney 1976, Solbrig 1976, Terborg 1979, Solbrig et. al. 1979, Mamaev and Semerikov 1981, Dirzo and Sarukhan 1984). Such coordination may also be of value in enabling forecast the future needs and research requirements of vegetation management.

Ecophysiology is the study of physiological mechanisms that adapt organisms to their environment; and the fate of the single plants then determines the fate of the population (Harper 1977). Population biology, which is concerned with the study of the processes that determine the size and composition of populations and that cause their establishment, growth and decline, therefore has many aspects in common with the ecophysiological approach. Jolls (1982) pointed out that, a major gap in our knowledge of alpine systems lies in our understanding of plant population biology, particularly the diversity of reproductive strategies and the biotic selective pressures which help shape these strategies. Solbrig (1976) argues that by integrating our knowledge of phenology, competition and reproduction, general predictions of plant response to environmental perturbations are made possible.

Some studies on arctic/alpine plants have centered around community classification and assessments of aboveground production by standing crop harvests (Wielgolaski 1972). Often, the underground organs have been studied in isolation from the shoots (Billings et al. 1973). Oberbauer and Billings (1981) pointed out that in conjunction with leaf characteristics, root system patterns are very important. These rooting differences and the diversity of habitats across topographic gradients interact to permit the maintenance of a diversity of plant species with different water and nutrient use patterns.

For alpine cushion plants little is known about both their physiological ecology and their population structure and dynamics. Recent reviews (Courtin and Mayo 1975, Bliss 1985) have shown the dearth of ecophysiological studies on plants of North America. The existing literature (Heilborn 1925, Hedberg 1964, Spomer 1964, Addison 1977, Izmailova 1977, Grabherr and Cernusca 1977, Moser et. al. 1977, Ralph 1978, Koerner and DeMoraes 1979, Fischer and Kuhn 1984) does not evaluate the ecophysiology of cushion plants in relation to their distribution in the alpine belt. Finally, most of the studies on arctic/alpine cushion plants were conducted in the arctic.

Objectives

The wide-ranging geographical distribution of cushion plants suggests a large degree of variability in their ecological behaviour, and the operation of different adaptive mechanisms. To obtain insights into some of the more important mechanisms governing the growth and survival of some alpine cushion plants, I have chosen the following six objectives:

1. To determine the range of distribution of the most common cushion plants on an alpine area of Mount Allan in the Rocky Mountains of Alberta.
2. To compare the phenology of cushion plants at different sites on the south- and the north-face of the mountain.
3. To describe their underground and aboveground parts, and determine the extent of site-dependent variation in root characteristics.
4. To investigate cushion plant reproductive strategies and compare resource allocation patterns.
5. To characterize seed germination biology and the extent of seedling growth and survival in the laboratory.
6. To investigate CO_2 gas exchange and plant water relations of different species, and identify leaf morphological and anatomical peculiarities related to gas exchange and water relations.

These objectives will be researched for their significance in cushion plant adaptation and local distribution in the alpine zone.

Hypotheses

The following six hypotheses were developed during the early stages of this study:

1. The rooting and resource allocation patterns of cushion plants with the same aboveground form are different and site-dependent.
2. The annual growing season of cushion plants is longer than that of other alpine vascular plants of this region.
3. Seed germination and seedling establishment play an important role for the distribution of alpine cushion plants.
4. Net photosynthesis is rather low, while the rate of dark respiration is relatively high.
5. The plant water relations of a species with a wide range of distribution are different from those of a species with a narrow range of distribution.
6. The relationship between cushion plants and their habitat is primarily a matter of survival and tolerance instead of perfect adaptation.

C. The Study Area

Location

Mount Allan (Plate 1.1a) in Kananaskis, Alberta, Canada (latitude 50°58'N, longitude 115°13'W) was selected as the study area (Fig.1.1) for the following reasons:

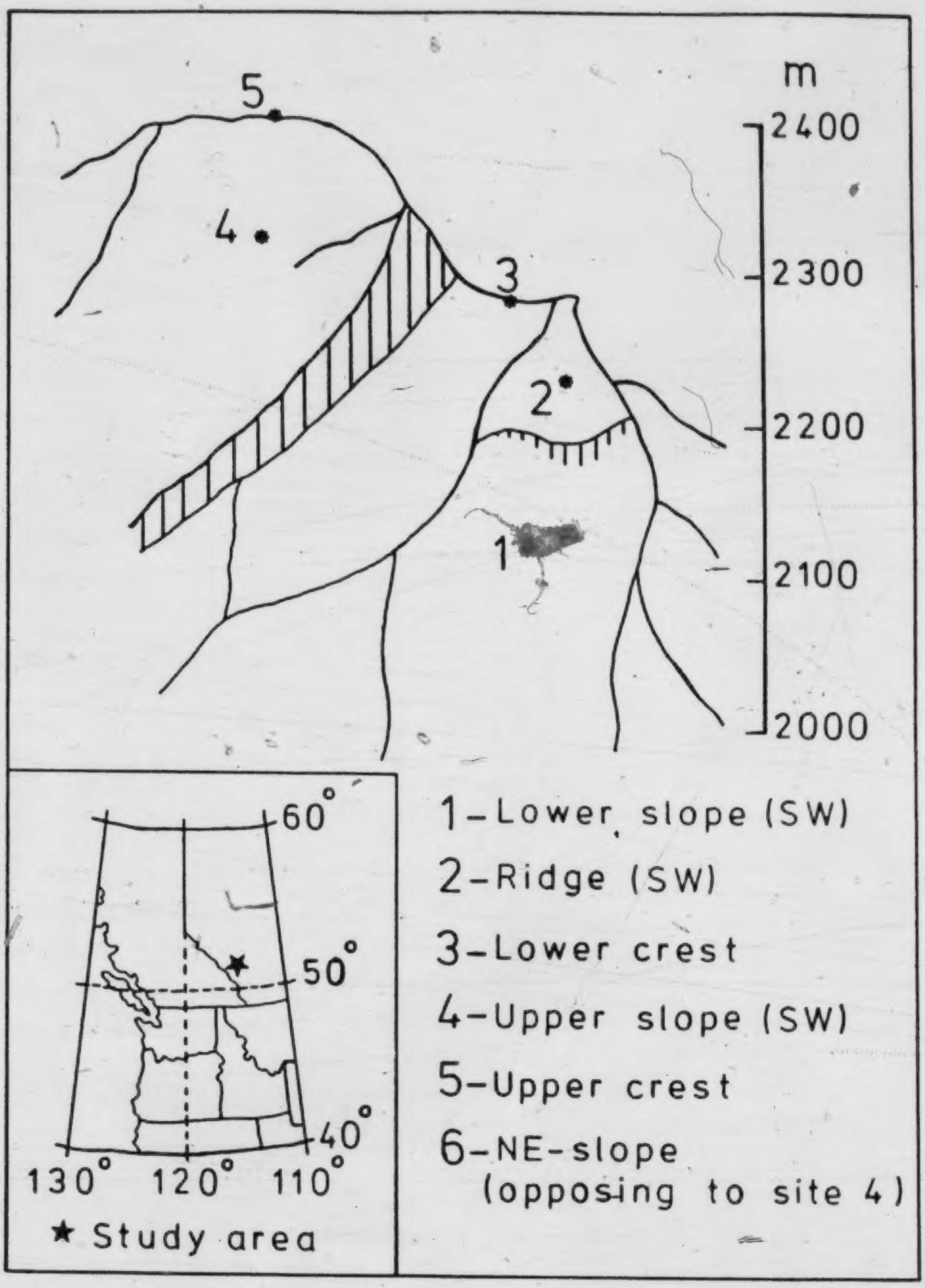
m
2400
2300
2200
2100
2000
1
2
3
4
5
60°
50°
40°
130°
120°
110°
★ Study area
1-Lower slope (SW)
2-Ridge (SW)
3-Lower crest
4-Upper slope (SW)
5-Upper crest
6-NE-slope
(opposing to site 4)

Figure (1.1): Profile view of the study area and site location on Mount Allan, Kananaskis, Alberta, Canada. Vertical lines indicate steep cliffs.

1. Some cushion plant species are abundant in this area, in an altitudinal gradient from 2030 to 2380 m above sea level (asl).
2. The study site is accessible (2 hour hike from the Kananaskis Highway).
3. The proximity of the Kananaskis Environmental Research Centre of the University of Calgary allows for the fast analysis of samples, if necessary, and provides room and board.
4. A variety of ecological studies have been carried out in the area of Mt. Allan, particularily in Marmot Basin, providing some relevant data for my research.

Geology

The structural geology of the Mt. Allan region has been described by Crockford (1949), Norris (1957), Bielenstein (1969), Stalker (1973), Gibson (1977), and Richards (1981). Only a brief description will be given here.

The mountain itself (2805 m) is composed of Mesozoic rocks. It has a well-developed synclinal structure capped by massive conglomerates of the Blairmore group. The conglomerates and other rocks of the Pocaterra member of the Blairmore group are lower Cretaceous in age and probably were freshwater deposits. Below these rocks lie the sandstones, conglomerates and shales of the coal-bearing Kootenay formation. This formation is mainly non-marine and Juro-Cretaceous in age. It overlies the Jurassic sandstones, siltstones and shales of the Fernie formation.

Soil

The soil is very rocky. The subaerial freeze-thaw weathering and mass-wasting processes, which are predominant over chemical weathering (Stalker 1973), have produced the broken, angular rubble on the slopes of different sites. The landscape has a steep slope topography (Wiken 1986). The southwestern side is exposed to the prevailing wind direction, and here surface erosion by wind is common. On the northeastern side, in contrast, wind-driven snow, landslides and snowslides seem to play an important role in soil development.

On the crest and on ridges, the bedrock is covered only with a jumble of large angular rock fragments which represent the first stage in the change from rock to soil. The bedrock is exposed in many places and the fine soil material is largely confined to pockets and cracks among the rocks or outcrops.

The upper slope is covered with a mixture of angular rock fragments, varying in size, and loose gravel, forming a cover which protects the underlying material that has accumulated among the boulders from transportation and erosion. Digging and burrowing animals are scarce, and the opportunity for mixing of soil and organic residues is therefore not as great here as on the lower slopes.

On the lower slopes, the soil is composed mainly of transported rock waste varying in texture. The rock fragments are contained within the soil profile. The material is less mobile and the xerosere has progressed until the last vestiges of the boulders have disappeared under the accumulating soil, which by now has become completely covered by vegetation (alpine meadow). A later stage is seen below the study site, where the vegetation is more luxuriant, frequently concealing the remnants of the disintegrating rock fragments.

On the NE-side slope, cool temperatures and moist conditions permit the accumulation of organic material. The rock fragments have mostly broken down and form, with the humus deposits, an even layer of soil which is well covered by the growth of low herbaceous vegetation with cushion plants.

The windblown dust may be an important addition to the scanty supply of soil material available to pioneer plants here. In the three years of observation a visible layer of dust accumulated on the surface of remaining snowflecks during the summer months.

Climate

Northeast-facing slopes of mountains in the northern hemisphere usually have a cooler and more humid microclimate than southwest-facing slopes (Haase 1970). The sun sets on an east slope shortly after the time of maximal air temperature, whereas west slopes are subjected to several hours of insolation during the hottest part of the day. Solar radiation increases with altitude and has a greater ultraviolet component. In addition, there is an increase in precipitation and wind speed towards the top of the mountain.

The climatic parameters of the study area were monitored with data obtained from two meteorological stations near the study area (Figure 1.2). At the Kananaskis station, the precipitation maximum occurs in summer during June (more than 100 mm.m^{-2}). The winter precipitation is less, but more evenly distributed. At Pocaterra, the precipitation shows a somewhat regular pattern, with maxima in May, August and December. The annual amount of precipitation is lower than at the Kananaskis station. The period with a monthly average temperature of more than 10°C lasts about four months at Kananaskis station, while it is only three months in Pocaterra. The air temperature exhibits wide seasonal variations at both stations, with about 25°C difference between the highest and the lowest mean monthly temperatures.

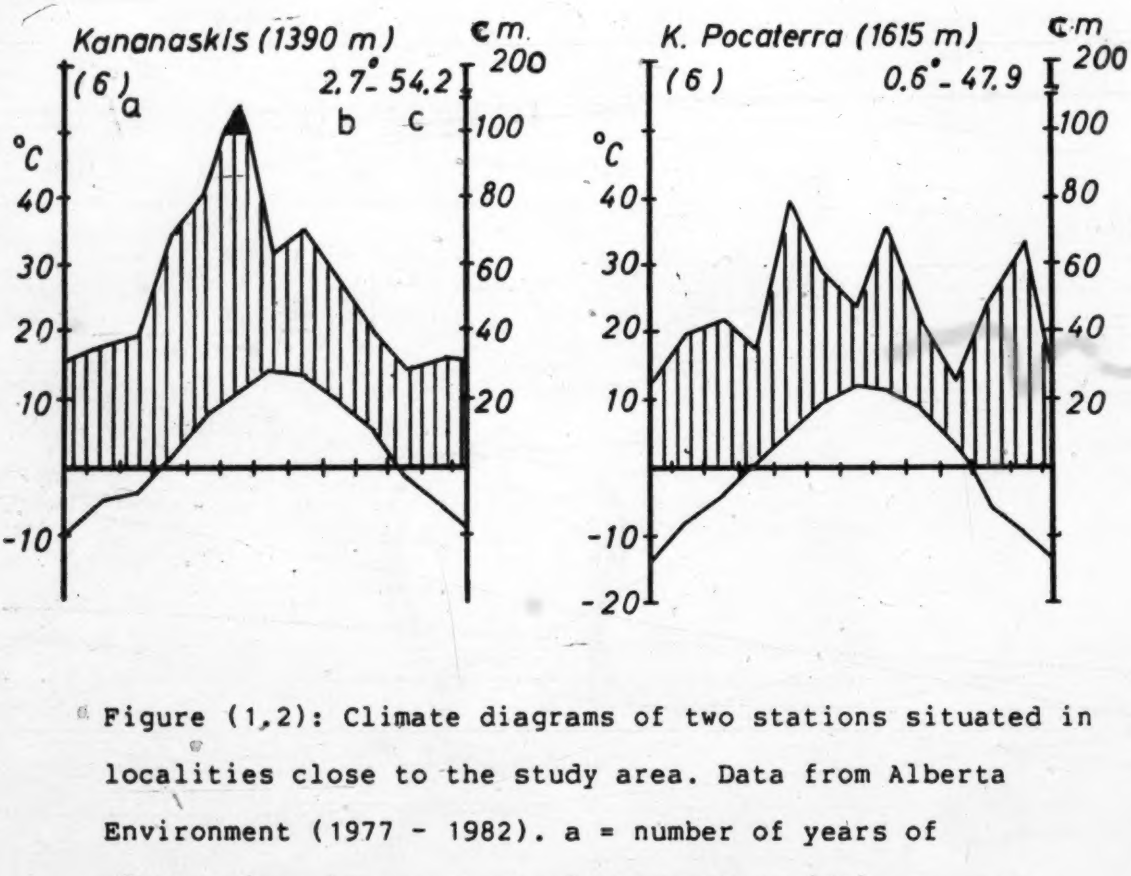

Figure (1,2): Climate diagrams of two stations situated in localities close to the study area. Data from Alberta Environment (1977 - 1982). a = number of years of observation; b = mean annual temperature (°C); c = mean annual precipitation (cm); vertical shading = humid season; black area = mean monthly precipitation > 100 cm (Scale reduced).

Vegetation

Cushion plants are common in the high alpine plant communities on Mt. Allan. These habitats are the driest and climatically most severe on the southwestern side. Mt. Allan has an open pioneer vegetation with a xerophytic plant cover due to factors such as severe wind erosion and rocky soil with low water holding capacity. At the same elevation, the northeastern side is characterized by a more luxuriant vegetation. Similar distributions of alpine plants have been described by many authors (Bliss 1956, Johnson and Billings 1962, Billings 1973, Hrapko and LaRoi 1978).

A common feature of cushion plant patterns is their growth side by side, forming stripes, arcs or bands known as "ripples". Such patterns have been described in semi-arid and arid zones (Ives 1946, Abdel-Rahman and El-Hadidy 1959, Boaler and Hodge 1962, White 1971) as well as in high mountains (Smith 1972, Bell and Bliss 1973). The vegetation ripples observed on Mount Allan (Plate 1.1), are separated by "lanes" and run either parallel to the inclination of the slope "downhill" or perpendicular to the prevailing wind direction. The ripples are richer in species than the intervening lanes and about 0.5 to 1 m wide. Their formation seems to depend initially on the arrangement and structure of the bedrock material.

0

Plate (1.1): General view of Mt. Allan and vegetation ripples of cushion plants. a - Mt. Allan (view from NE side). b - Vegetation ripple of *Eriogonum androsaceum*. Note the grass invasion. c - Mixed vegetation ripple of *Eriogonum androsaceum*, *Potentilla uniflora*, *Saxifraga caespitosa*, and the non-cushion plant *Potentilla fruticosa* L. d - Mixed vegetation ripple of *Potentilla fruticosa* invaded by *E. androsaceum*, *P. uniflora*, *S. caespitosa*, and grasses.

a
b
c
d

D. Study Species

The following six species were selected for this study. Species nomenclature follows Moss (1983).

1. *Eriogonum androsaceum* Benth. (Polygonaceae). It grows on rock slides and exposed summits at high altitudes, and its distribution is restricted to southern British Columbia, and Alberta south to Montana. Figure(1.3) and Plate (1.2a).
2. *Potentilla uniflora* Ledeb. (Rosaceae). It grows on dry rocky alpine slopes. Somatic chromosome number 2n = 28. Distributed in Siberia and Alaska; Yukon, District of Mackenzie south to British Columbia, west Montana, Colorado, northwest Hudson Bay. Figure (1.3) and
3. *Saxifraga caespitosa* L. (Saxifragaceae). Common on most alpine banks and rocky ledges. Somatic chromosome number 2n = 80. Circumpolar distribution: Alaska, Yukon to Ellesmere Island; also in Newfoundland; south to Oregon, Nevada, Utah, New Mexico; District of Mackenzie, Hudson Bay, north Quebec, Gaspe. Figure (1.3) and Plate (1.2c). Plate (1.2b).
4. *Saxifraga bronchialis* L. ssp. *austromontana* (Wig.) Piper. (Saxifragaceae). Common on not too dry cliffs and in somewhat shaded crevices among rocky outcrops, ascending from montane to alpine elevations. Somatic chromosome number 2n = 26.

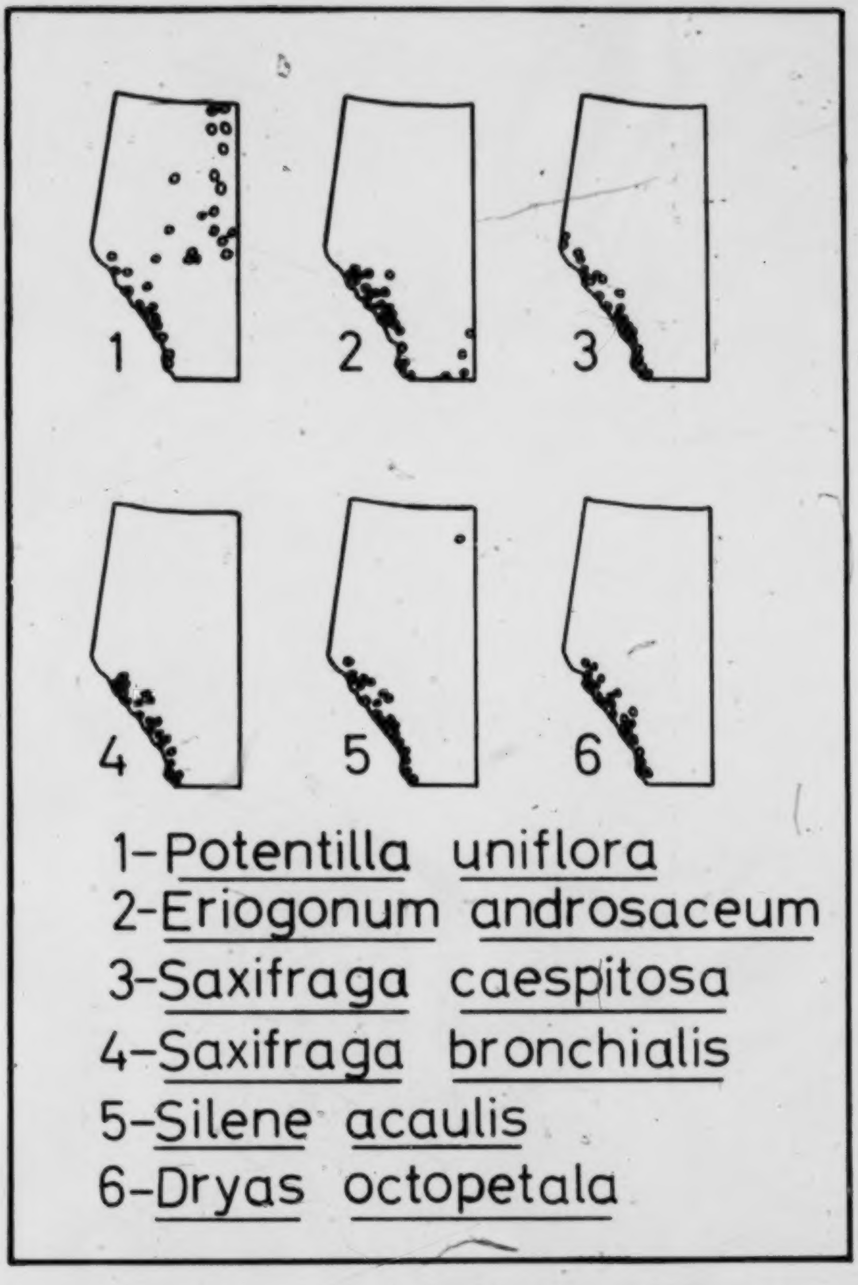
1
2
3
4
5
6
1-Potentilla uniflora
2-Eriogonum androsaceum
3-Saxifraga caespitosa
4-Saxifraga bronchialis
5-Silene acaulis
6-Dryas octopetala

Figure (1.3): Dot maps showing the distribution of the six cushion plant species in Alberta (after Moss 1983).

Plate (1.2): The six study species. (a) *Eriogonum androsaceum* Benth. (b) *Potentilla uniflora* Ledeb. (c) *Saxifraga caespitosa* L. (d) *Saxifraga bronchialis* L. (e) *Silene acaulis* L. (f) *Dryas octopetala* L.

a
b
YASHICA
c
d
e
f

Distribution: Asia; Central British Columbia, Alberta south to Washington, northeast Oregon, Idaho, Utah, New Mexico. Figure (1.3) and Plate (1.2d).

5. *Silene acaulis* L. var. *exscapa* (All.) Dc.(Caryophyllaceae). Common in rocky and turfy alpine locations. Somatic chromosome number 2n = 24. Circumpolar distribution: Alaska, Ellesmere Island to Newfoundland, south to Oregon, Arizona, New Mexico, southwest District of Mackenzie, James Bay, northern Quebec, New Hampshire. Figure (1.3) and Plate (1.2e).
6. *Dryas octopetala* L. ssp. *hookeriana* (Juz.) Hult. (Rosaceae). Grows mainly on xeric alpine slopes. Somatic chromosome number 2n = 18. Its distribution is more or less circumpolar: Alaska to Melville Islands south to Washington, northeastern Oregon, Idaho, Montana, Colorado. Figure (1.3) and Plate (1.2f).

E. Summary

Cushion plants are perennial chamaephytes widely distributed on the globe. They are growing commonly on high mountains of all parts of the world, as well as in the arctic, subantarctic, and in deserts.

Few species of cushion plants have been studied in detail, and published accounts of research on their autecology and population biology are considered limited.

For this study six hypotheses have been developed; a study area has been established on Mount Allan, Alberta, from 2030 m to about 2380 m asl.

The six study species are *Potentilla uniflora* Ledeb., *Eriogonum androsaceum* Benth., *Saxifraga caespitosa* L., *Saxifraga bronchialis* L., *Silene acaulis* L., and *Dryas octopetala* L.

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II. Species Distribution and Cushion Plant Cover Structure

A. Introduction—

The species distribution in plant communities of temperate climates was studied by many authors, as reviewed by Whittaker (1969 and 1972). Ogilvie (1962) found two major groups of plants growing in the Rocky Mountains of Alberta: One group, commonly refered to as boreal, extends northward, then eastward across the northern part of the continent. The second group is largely confined to the cordilleran portion of western North America.

In alpine areas, the distribution of plants mainly depends on the topography. Climatic factors such as radiation, wind, temperature, snow cover, etc. are influenced by relief, and the microenvironmental conditions may therefore vary considerably even within a very restricted area (Daubenmire 1943, Billings 1952, MacArthur 1972, Kuchar 1975, Douglas and Bliss 1977, and Klug-Puempel 1982). The snow is swept away by the wind, from ridges, crests, and peaks, and is left in depressions and valleys. The drifted snow accumulates on leeward slopes and remains as snowbanks into early or even late summer. This uneven distribution of snow is repeated every year. The amount of snow may vary considerably, but the distribution is about the same (Bliss 1956, Gjaerevoll and Bringer 1965, Mark and Bliss 1970, and Swanson 1986). Cushion plants in areas that are snowfree early must withstand low temperatures, late summer drought, and heavy wind erosion. These species are expected to be xerophilous, as they experience severe desiccation. On the other hand, snow-bed cushion plants experience a reduced growth period. They are not exposed to particularly low temperatures.

In this chapter, the distribution of the six most common alpine cushion plants on Mount Allan (*Eriogonum androsaceum* Benth., *Potentilla uniflora* Ledeb., *Saxifraga caespitosa* L., *Saxifraga bronchialis* L., *Silene acaulis* L., *Dryas octopetala* L.) will be described. Since the distribution of cushion plants seems to be influenced not only by soil moisture and temperature, but also by the prevailing wind, due consideration will be given to the role of all three of these factors.

B. Methods

Soil: For the determination of soil moisture, three replicate samples were collected from the various sites at depths of 0 - 5 cm, 5 - 10, 10 - 20 and 20 - 30 cm, and placed in tightly closed plastic bags for fresh weight determination. The samples were then air dried in the laboratory for two weeks and reweighed several times until constant weights were obtained. The soil moisture content was calculated on air dry basis.

Climate: The microclimate measurements were taken at the field sites. Wind speed was measured with a 3-cup hand anaemometer. Each value shown in Figure (2.2) is the average of five readings. Soil temperature, plant temperature, and air temperature were measured with thermistors.

The soil and plant temperatures were taken from one individual cushion plant.

Vegetation: The vegetation was studied according to the Quadrat-Charting Method described by Mueller-Dombois and Ellenberg (1974; Pg. 81-83). To determine how the distribution of cushion plant species varies along environmental gradients such as elevation, topography, and aspect, three transects were laid up-slope across the sites of the study area, and the cushion plant species occurring along these transects were recorded. The percentage of every species at various sites in relation to the total number of cushion plant species (relative density) was estimated. To estimate the cushion plant cover structure, 5 x 5 m quadrats were mapped at various sites along the transects. This was done by dividing the 5 x 5 m quadrats into 25 (1 x 1 m) square meters. Shoot outlines of the area occupied by individual cushion plants were recorded on graph paper. The species and the number of individuals per cushion plant species were recorded.

C. Results

Soil Moisture

On the SW side, a lower soil moisture content was found during the whole growing season (Figure 2.1).

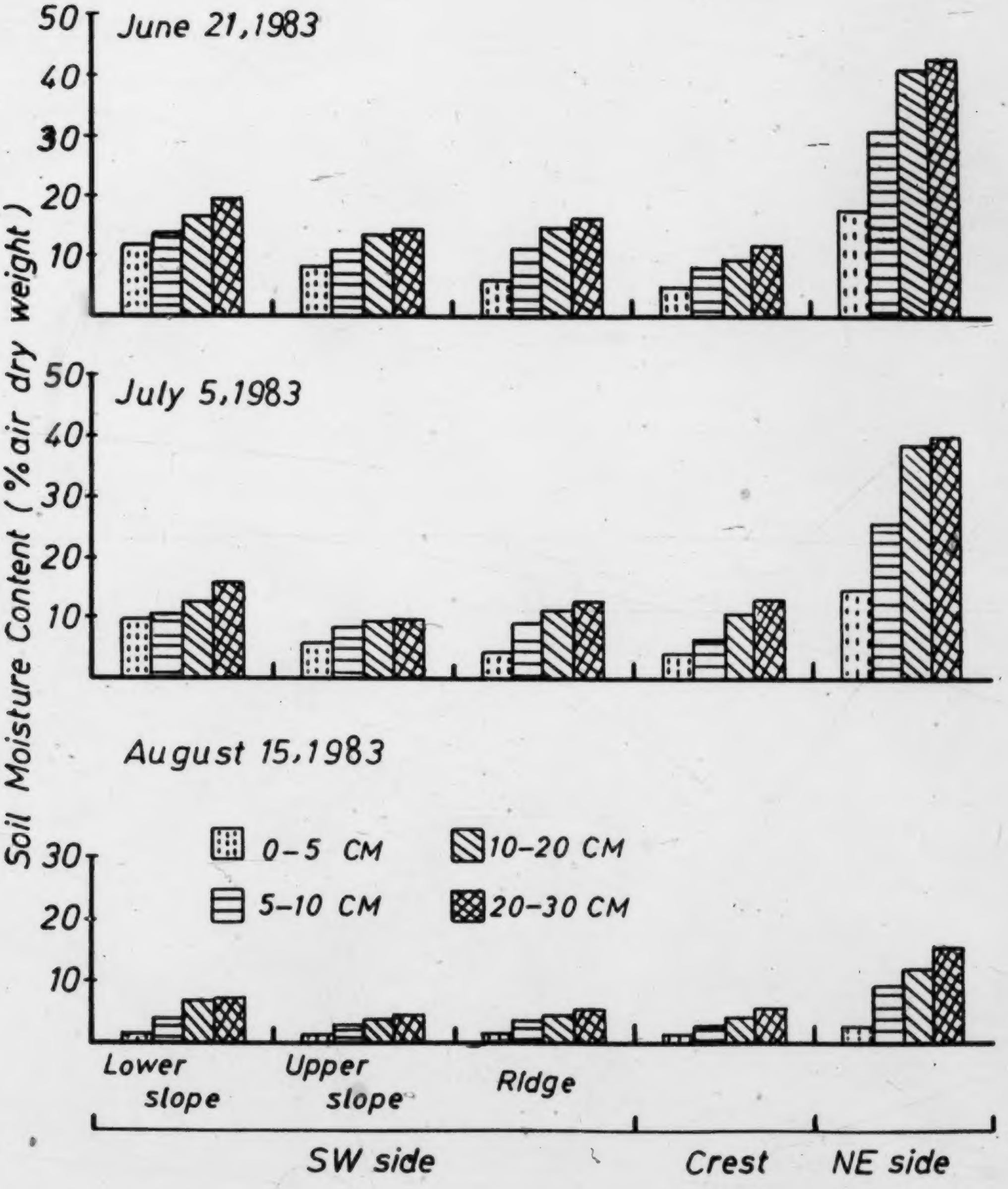

Figure (2.1): Soil moisture content at successive depths in five sites of the study area.

Soil moisture at the various sites tends to increase with depth. On the crest, the snow is blown away and accumulates on the NE side, which increases the soil moisture content there (Appendix 1). The snow is also blown off the slopes of the SW side. Together with the drying effects of strong winds, solar radiation and soil conditions, this produces lower soil moisture amounts there.

The lower slope on the SW side retains soil moisture far better than both the upper slope and the ridge. This is partly due to the finer material and humus incorporation, which increases the water holding capacity of the soil.

Wind

In alpine regions, wind is often an important or dominant factor in controlling the growth and character of the vegetation. The wind measurements show that on both the NE and SW side, wind speed doubles or triples within the first few meters above ground. Wind speed on the SW side was several times that of the NE side at the various heights and at different times of day (Figure 2.2; Appendix 2).

Since cushion plants are characteristically low growing, the foliage lies in a layer near to the ground where wind speeds are reduced. But cushion plants contribute substantially to the roughness of the surface (Warren-Wilson

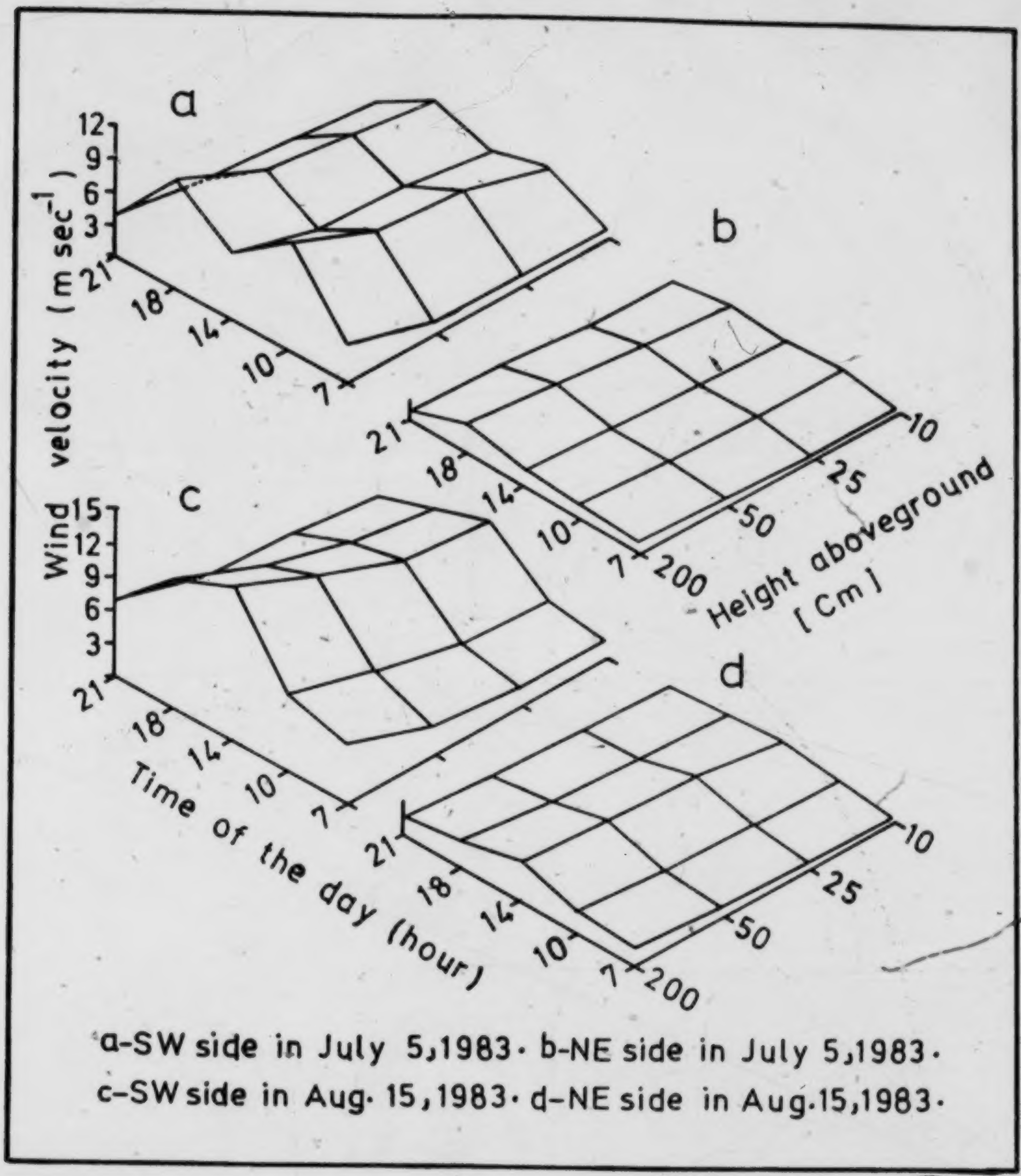

Figure (2.2): Daily course of wind velocity with height aboveground on both southwest and northeast sides of Mt. Allan.

1959, Price 1981), causing turbulence and high variations in wind speed. On clear summer days the typical change of the wind direction, as described for N-S oriented valleys by Defant (1951), can be observed regularly on Mt. Allan. During the night and in the morning a cool breeze blows steadily from the south, keeping temperatures low. At about 13:00 the direction of the wind changes rather abruptly, putting the SW slope in the lee for the next seven to eight hours.

Temperature

Since the amount of radiation received depends on the angle of the sun's rays, the daily fluctuation in temperature varies with slope, exposure and aspect, in addition to other factors like wind, clouds, precipitation, etc. The more obliquely the rays strike, the less light is received per unit area, until at an angle of 10° a given uniform area receives only 17% of the radiation at 90°. Since cushion plants are close to the ground and oriented parallel to the slope, inclination and aspect influence their temperature regime much more than that of larger erect plants.

Figure (2.3) illustrates differences between ambient air, cushion plant, and soil temperatures (Appendix 3). Generally, the domed shape of cushion plants reduces the plant's surface-to-volume ratio, which would conserve energy (Ralph 1978). This causes the plant to heat up

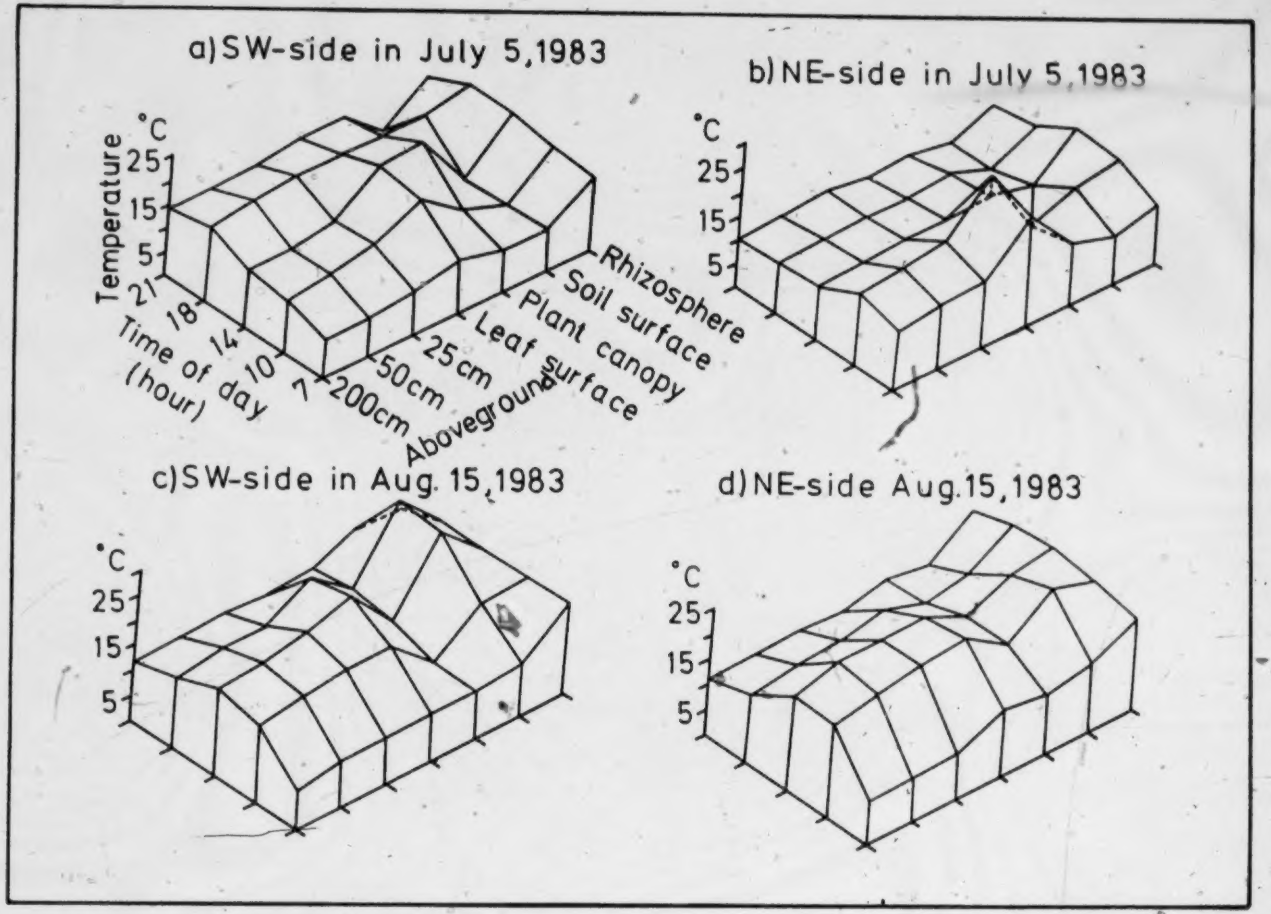

Figure (2.3): Daily course of soil, cushion plant and air temperatures on southwest (*Eriogonum androsaceum*) and northeast (*Saxifraga bronchialis*) sides of Mt. Allan.

more than the air surrounding it (Fischer and Kuhn 1984). During the daytime, heat is stored in the plant body and between the shoots.

Vegetation

The relative density and cover values of the six cushion plant species were compared along an elevation gradient at the various study sites (Tables 2.1 and 2.2). The lower slope has the lowest number of species and the lowest total number of all cushion plant individuals, while the ridge and the crest showed the highest number of species. The ridge is unique in having both the highest number of species and highest total number of individuals, that is, the highest species richness (expressed as average number of species per site).

The different species seem to appear and disappear independently as one goes up from the lower slope on the SW side over the crest to the NE side (Figure 2.4). *E. androsaceum* and *P. uniflora* occupy the widest range of distribution on the SW side. In contrast, *S. caespitosa* is represented by very few individuals and has the lowest relative density of all cushion plants. *S. bronchialis* and *S. acaulis* dominate at the NE side and extend to the SW side over the crest. They show their highest relative density at the NE side (Table 2.1). *D. octopetala* grows only on the NE side and the crest.

Table (2.1): Cushion plant species distribution (mean absolute numbers and relative density, n=9) along three line transects down-up slope on five sites of the study area. Absolute numbers were estimated per 25 m length of the transect at every site. Absolute numbers are rounded to the nearest whole number. Absolute lowest and highest values in parentheses.

Species			SW-SIDE				CREST		NE-SIDE	
	lower slope		upper slope		ridge					
	abs. #	rel. dens.	abs. #	rel. dens.	abs. #	rel. dens.	abs. #	rel. dens.	abs. #	rel. dens.
E. androsaceum	7 (3-11)	87.5	16 (11-19)	53.3	10 (7-12)	29.4	3 (0-5)	11.6		
P. uniflora	2 (0-4)	12.5	09 (5-13)	30.0	17 (12-20)	50.0	5 (2-8)	19.2		
S. caespitosa			02 (0-3)	06.7	02 (0-3)	05.9				
S. bronchialis			03 (1-5)	10.0	04 (0-7)	11.8	3 (1-5)	11.6	4 (1-5)	22.2
S. acaulis					01 (0-3)	02.9	5 (2-7)	19.2	4 (2-5)	22.2
D. octopetala							?	?	?	?

0

Table (2.2): Density and cover of six cushion plant species in 15 releve plots (5 x 5 m) at five sites in the study area. Three replicates for each releve. SW = Southwest, C = Crest, NE = Northeast, LS = Lower Slope, UP = Upper Slope, R = Ridge. Absolute numbers are rounded to the nearest whole number. Absolute lowest and highest values in parentheses.

Species	Aspect Site Releve	SW LS 1	SW LS 2	SW LS 3	SW US 4	SW US 5	SW US 6	SW R 7	SW R 8	SW R 9	C 10	C 11	C 12	NE 13	NE 14	NE 15
								a-density data								
E.androsaceum		8 (4-11)	7 (3-10)	8 (5-10)	6 (5-8)	7 (4-8)	12 (10-15)	9 (7-13)	7 (6-9)	10 (7-15)	2 (1-3)	0 (0)	1 (0-3)			
P.uniflora		2 (0-4)	1 (0-2)	3 (1-4)	9 (6-11)	8 (7-10)	16 (11-19)	15 (12-19)	9 (7-18)	10 (8-11)	3 (2-5	3 (1-4)	3 (1-4)			
S.caespitosa					1 (0-2)	2 (0-2)	2 (1-3)	3 (1-4)	2 (0-2)	3 (2-4)						
S.bronchialis					2 (1-3)	2 (1-3)	1 (1-2)	3 (2-5)	2 (0-3)	2 (1-3)	2 (1-4)	1 (0-3)	1 (1-3)	4 (2-5)	3 (1-4)	3 (2-4)
S.acaulis								1 (0-2)	1 (0-2)	0 (0)	3 (2-3)	3 (2-4)	2 (1-4)	1 (0-3)	3 (2-5)	2 (1-4)
D.octopetala											?	?	?	?	?	?
								b-percentage cover data								
E.androsaceum		6.3	3.9	6.6	5.1	4.2	3.3	3.7	3.2	3.4	2.6	0.0	1.7			
P.uniflora		1.1	0.8	1.5	4.8	6.9	7.8	5.3	2.4	4.7	1.7	1.2	1.1			
S.caespitosa					0.3	0.3	0.3	0.4	0.4	0.5						
S.bronchialis					1.1	0.6	0.5	0.8	0.5	0.6	0.5	0.2	0.3	1.1	0.9	0.4
S.acaulis								0.5	0.4	0.0	1.5	1.2	0.6	0.9	0.9	0.6
D.octopetala											58.5	36.0	31.5	48.3	52.5	30.0
Total % cover		7.4	4.7	8.1	11.3	12.0	11.9	10.7	6.9	9.2	64.8	38.6	35.2	50.3	54.3	31.0

The comparison of the species distribution based on the number of individuals with that based on cover percentage (Table 2.2) does not show clear differences at most of the sites and the six species have approximately the same distribution patterns. However, the sampling areas on the ridge and the crest showed the highest number of species, while the cover percentage is greatly reduced at the ridge.

The total cushion plant cover percentage in the 15 releves (Table 2.2) varied widely among sites. Ranging from 4.7% on the windward side up to 54.3% and 64.8% on the leeward side and the crest, it never exceeded 65%. In agreement with the findings of Armesto et al. (1980), the cover percentage values of the same species varied markedly at different sites of the study area. High cushion plant cover is developing on the lee slopes and the crest not only because of better soil conditions and the absence of direct mechanical damage due to waste rock movement, but also due to greater protection against desiccation.

The estimated total vascular plant cover percentage in the study area varied among sites. It ranged from 65% on the NE-slope to about 25% on the crest. On the SW-side, the percentage was 20% on the lower slope, and 15% at the upper slope. On the ridge it was 8%.

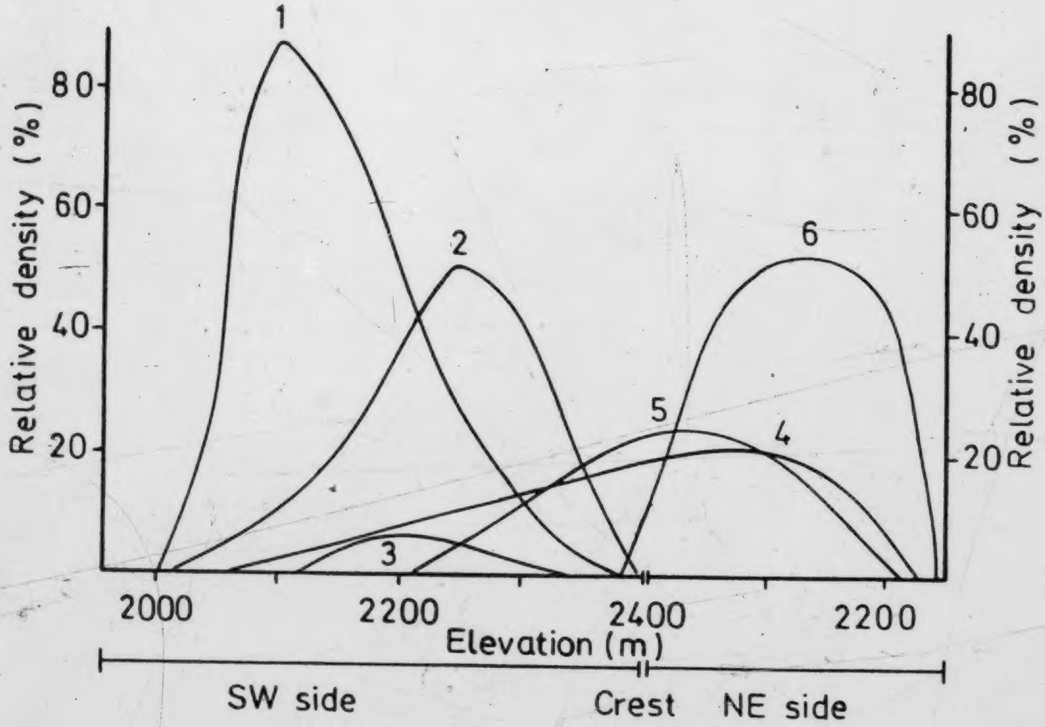

Figure (2.4): The distribution of cushion plants along the elevation gradient on Mt. Allan. 1 - *Eriogonum androsaceum*. 2 - *Potentilla uniflora*. 3 - *Saxifraga caespitosa*. 4 - *Saxifraga bronchialis*. 5 - *Silene acaulis*. 6 - *Dryas octopetala*. Data modified from tables (2.1) and (2.2).

The distribution of cushion plants in the study area shows four different patterns:

1. Two species (*Eriogonum androsaceum* and *Potentilla uniflora*) are growing over a broad range all along the soil moisture gradient on the main windward side of Mt. Allan.
2. *Dryas octopetala* and *Silene acaulis* grow on the lee side or on protected microsites of the crest with low wind action and higher soil moisture.
3. *Saxifraga bronchialis* occurs discontinuously along the altitudinal alpine gradient on both windward and lee sides. This species needs fine, moist soil, present in protected microsites among rocky outcrops.
4. *Saxifraga caespitosa* is restricted to sheltered rocky microsites on the SW slope, and therefore has a very restricted local distribution.

A common property can ~~be~~ derived from the species distribution pattern, either based on number of individuals or on cover percentage: The variation in cushion plant distribution corresponds closely to changes in topography, exposure and aspect. On wind-swept ridges with no or scanty snow cover in winter, there is a low cushion plant cover. With decreasing exposure the areas of bare soil and soil erosion disappear, and the cushion plant cover becomes better closed.

D. Discussion

The complex interaction of different environmental factors (Billings 1952) in relation to slope and aspect leads to a variety of different microhabitats in the alpine region (Shreve 1924, Geiger 1975). This fact favours disruptive evolution (increase of population variation) and eventually produces a number of different plant communities. In the alpine zones, topographic moisture gradients are the consequence of an uneven distribution of winter snow (Oberbauer and Billings 1981). Such gradients are represented many times in a single mountain range.

Wind is an ever-present environmental factor in both arctic and alpine tundra (Defant 1951, Bliss 1956), and frequently influences the distribution of mountain plants (Pears 1967, Naegeli 1971, and Scott 1977 a and b). The cushion plant distribution in habitats exposed to wind on the SW side of Mt. Allan is different from that on the NE side. The highest cushion plant species richness is attained on the exposed ridges of the SW side, where strong regular winds prevail. The dense and compact growth of the cushion here can be regarded as the most resistant form against strong winds (Braun-Blanquet 1951).

The quick and often dramatic change over short time periods of environmental conditions such as moisture, mechanical soil characteristics etc., typically puts the alpine plant into a rather unstable situation (Salisbury and Spomer 1964). The compact and dense growth of cushion plants ameliorates these conditions and leads to a higher level of stability. In turn, the stabilization of soil temperatures influences root metabolism, mineral nutrition and translocation processes in the plant positively (Anderson and McNaughton 1973).

Generally speaking, the cushion growth form must be considered advantageous in certain microhabitats of the alpine zone, although opinions about these selective advantages vary among authors (Rauh 1939, Hedberg 1964, Billings 1974). In conclusion, the soil moisture, wind, and temperature together with other factors play a leading role for the distribution of cushion plants in the alpine zone of Mt. Allan.

E. Summary

The six dominant cushion plant species on Mt. Allan are unevenly distributed. *Eriogonum androsaceum* and *Potentilla uniflora* dominate the windswept SW slope from dry to mesic soil conditions. *Dryas octopetala* prefers the lee side, while *Silene acaulis* grows best on the crest. *Saxifraga bronchialis* grows only on moist fine soil, present on both windward and lee, and *Saxifraga caespitosa* occurs on the windward slope in sheltered rocky microhabitats.

The lee side has a higher cushion plant cover probably due to better soil development and water supply and less solifluction.

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III. Phenology

A. Introduction

Phenological studies provide information on functional rhythms of plants and plant communities (Ralhan et al. 1985), where various phenological events may be timed to biotic and/or abiotic environmental conditions (Lee 1971 and Estabrook et al. 1982). The literature on phenological research in many parts of the world has been reviewed by Soerensen (1941), Narinyan (1960), Savile (1964), Holway and Ward (1965), Clarke (1968), Mark (1968 and 1970), Bell (1974), Lieth(1974), Wielgolaski and Kaerenlampi(1975), Bell and Bliss (1977), Arroyo et al. (1981), McGraw et al. (1983), and Jackson and Bliss (1984). For cushion plants, the dearth of phenological studies in alpine zones has been pointed out by some authors (see Lieth 1974). Only a few analyses of leafing, flowering and fruiting are available for a limited number of alpine species. Because of the lack of information in the literature, it is difficult to assess, in general, the hypothesis that phenological characteristics of alpine cushion plants may influence their local distribution patterns.

Soerensen (1941) distinguishes three main phenological strategies: 1) Winter-green species - leaves begin to develop and partially expand during one summer, mature in the following summer and die at its end. 2) Summer-green species - leaves develop and complete their lives during a single summer. 3) Evergreen species, which function for more than two summers. The winter-green and evergreen phenological strategies represent an adaptation to a short, cold growing season in the alpine zone (Bell and Bliss 1977), in that plants are ready to begin photosynthesis in the spring, with minimal time spent in leaf expansion.

According to Rathcke and Lacey (1985), the seasonal timing of life cycle events of terrestrial plants can be critical to their survival and reproduction. Hoffmann and Walker (1980) pointed out that the influence of seasonal behaviour on the ability of a species to spread can be analyzed by the knowledge of phenology and some aspects of water relations. However, some ecologists have only recently paid attention to the relationship between phenological patterns, vegetative growth strategies and reproductive characteristics (Arroyo et al. 1981).

Alpine plants are well known for the speed with which they complete their reproductive cycle - an obvious adaptation to the short growing season. In general, they come into flowering and fruiting more rapidly than most non-alpine plants. The great variety of edaphic and climatic conditions in the high mountains, as well as that of the microhabitats due to variation in topography and exposure, induce different phenological behaviour not only among the different species, but also within the same species, even at the same altitude. Generally, snow cover and soil moisture are found to be primary factors influencing tundra phenology

(Cox 1933, Billings and Bliss 1959, Holway and Ward 1963 and 1965), with temperature and photoperiod also of great importance (Soerensen 1941, Billings and Mooney 1968). According to Holway and Ward (1965) and Wielgolaski (1974) slope and aspect are distinctly secondary in their influence on phenophases of high mountain plants. This is in contrast to the findings of Bliss (1956).

The study area for this paper comprises several different microhabitats, distinguished by variations in topography, exposure and aspect. Each habitat has its own set of local environmental factors, and the availability of soil moisture during the growing season varies in the different sites due to the variability in snow cover during the winter. Swanson (1986) described the seasonal development of the snow cover of nearby Marmot Basin. The dry snow of early winter and midwinter is easily transported by the wind, thus exposing the plants, except for areas where accumulated snow is protected from wind action by rock obstacles. The snow that falls during spring is wetter and more cohesive and resists wind erosion.

B. Material and Methods

During the growing season of 1984, six phenological sampling sites were established in the study area on Mount Allan. The sites range from 2100 m to 2360 m asl in elevation, and vary considerably in exposure, slope angle and vegetation cover. The study area sampling sites are described in Table (3.1).

To facilitate the periodic observations of phenological phases three line transects were set up in every sampling site, running parallel to the slope, and were marked with wooden stakes. All cushion plants occurring within two meters on either side of the transect line were examined. Observations were made on the same plants on May 24, June 20, July 12 and August 24, 1984. In site III, observations of May 24 began on snow-free troughs, while many other areas were still covered by drifted snow. Where feasible, 10 individual plants of every species was observed along every transect at each site (i.e. 30 individual plants per species at each site), with the exception of *S. caespitosa* , of which fewer plants were found. For *D. octopetala* 30 observations of plant carpets (0.16m^2 each) were made.

The periodic phenological observations were carried out according to the technique adopted by West and Wein (1971). This method provides numerical ratings of closely defined phenological phases. The recorded phenophases are given in Table (3.2).

The phenological index score consists of two parts. The number to the left of the point denotes the phenophase; the number to the right of the point indicates the percentage to the nearest 10% of the plant parts that have developed past the indicated phase. For example, if the plant has barely begun to flower, a score of (4.1) would be recorded.

Table (3.1): Characteristics of study area sites.

Site	Altitude (m)	Aspect	Slope angle	Vegetation cover
I (Lower slope)	2100	SW	34	20%
II (Ridge)	2225	SW	22	08%
III (Lower crest)	2240	—	—	25%
IV (Upper slope)	2315	SW	30	15%
V (Upper creat)	2360	—	—	28%
VI (Northern slope)	2325	NE	25	65%

Table (3.2): Phenological phases and their corresponding base scores.

Base score	Phenophase
1	Dormancy/bud swelling
2	Expanding leaves (leaf appearance)
3	Shoot elongation (mature leaves)
4	Floral bud-developing
5	Flower opening
6	Fruiting (fruit development)
7	Fruit maturation (seeding)
8	Senescence (die-back)

The base score of (4) would indicate that the plant was in the floral bud-developing phase, while (1) denotes that only about 10% of the buds with flowering potential have opened. Only when 100 percent of the plant reaches a given phase will the plant be given a whole number base score.

Phenophases were defined subjectively in the course of making the observations, following Murray and Miller (1982). Expanding leaves were those which were still emerging from the buds and held in an upright position. The mature or expanded leaves with the appearance of petioles (if any) indicated the shoot elongation phase. The presence of the flower bud-developing was defined as the period from slight bud enlargement to breaking of the bud. Flower opening was defined as the perianth parts exposed. This criterion was used whether the plant bore a solitary flower or inflorescence. Loss or die-back of petals and stamens denoted fruiting. The dispersal of seeds or dry fruits indicated seed or fruit maturation. Senescence was noted by colour change and leaf die-back.

Other observations were taken, such as counting the number of expanded green leaves and the number of die-back (yellowing or drying) leaves per single shoot or branch (Five branches were chosen randomly on every observed plant). The total number of flowers or inflorescences per individual plant was counted. The average diameter of the crown of every observed individual plant was also measured.

C. Results

Dormancy was broken in spring at rather low temperatures, although initiation of the growing season varied among the different species. Plants on the SW side at lower elevations developed more rapidly than plants at high elevations and plants on the NE side. In contrast, shoot senescence coincided with the onset of seed set in late summer, regardless of the site location or species. In *E. androsaceum* a shoot dimorphism was sometimes found, where relatively long shoots grew exceptionally rapidly. These shoots terminate the growing season with swollen buds, which are either destroyed in the course of the winter or sprout early in the succeeding spring. The wintering buds are concealed and/or protected by the withered or dead leaves which remain attached to the shoots. In *S. acaulis*, the compact wintering buds are protected by the closely packed leaves of the bud, where the old withered leaves have been turned aside, leaving the bud visible.

The average phenological indices shown in Figure (3.1) and Table (3.3) demonstrate the similarities and also variations in the length of phenological phases maintained by different species at various sites. Although species varied considerably with regard to the length of time involved in a given phenological phase, they all showed more or less general consistency in seed maturation by the end of August, that is,

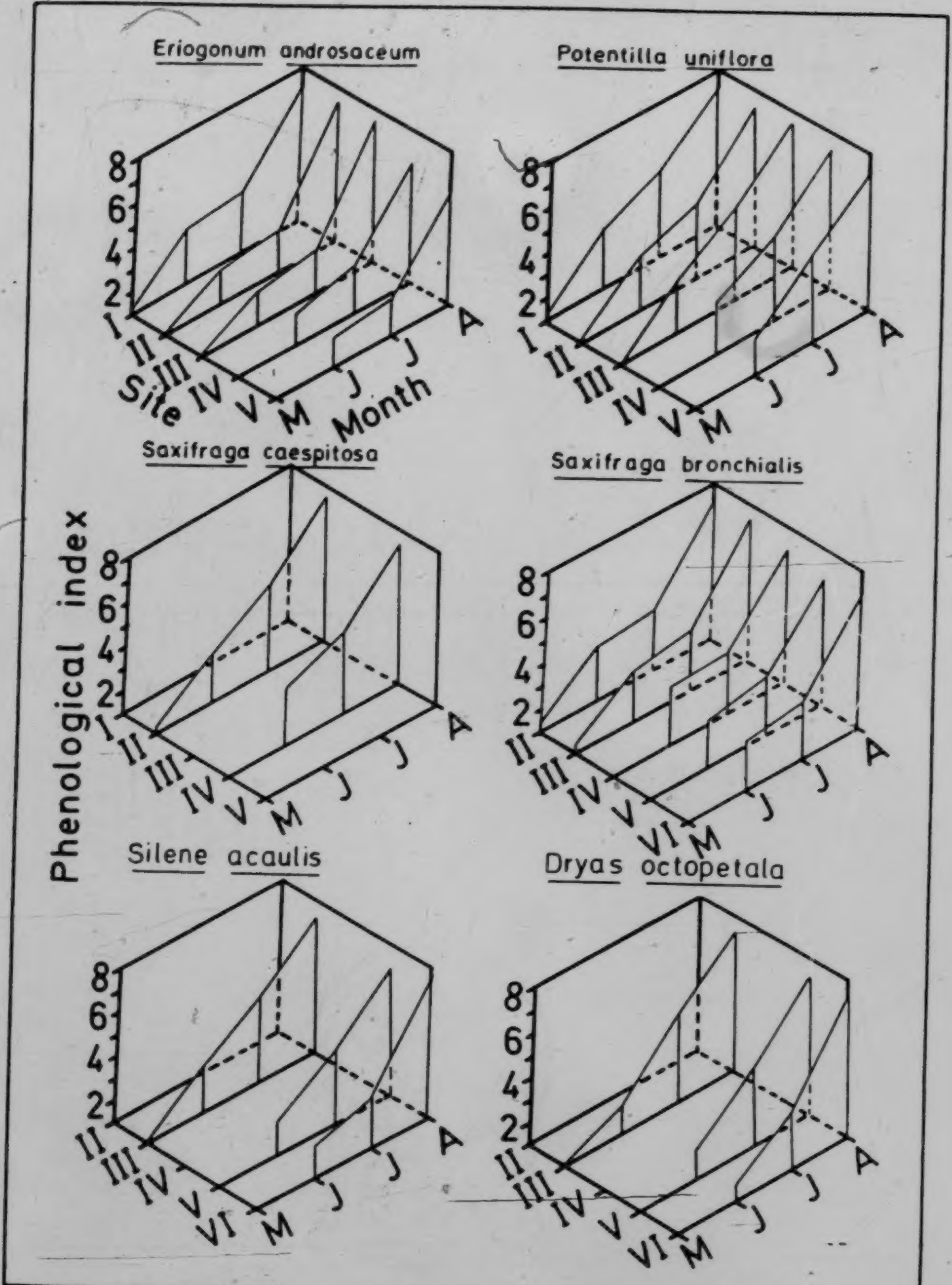


Figure (3.1): Plant phenological index of the studied species at various sites in May, June, July and August of 1984.

Table (3.3) The range of variability (absolute lowest and highest values) in phenological indices of the investigated species at the six study sites during the 1984 growing season.

Species	Site					
(month)	I	II	III	IV	V	VI
Eriogonum androsaceum						
May	1.1-1.2	1.0-1.0	1.0-1.0	———	———	
June	3.2-3.8	2.6-2.9	2.4-2.8	2.1-2.7	2.2-2.4	
July	3.8-4.1	2.7-3.3	2.8-4.1	2.9-3.4	2.5-2.7	
August	7.1-7.4	7.2-7.3	7.2-7.8	5.9-7.2	5.7-6.2	
Potentilla uniflora						
May	1.0-1.4	1.0-1.2	1.0-1.0	———	———	
June	3.8-4.2	3.3-4.1	2.9-3.7	3.1-3.6	2.5-2.8	
July	4.5-5.3	4.2-5.2	4.4-5.7	4.4-5.2	4.4-5.1	
August	7.2-7.3	7.2-7.5	7.1-7.6	7.1-7.3	6.8-7.4	
Saxifraga caespitosa						
May		1.1-1.4		———		
June		2.7-3.5		3.1-4.4		
July		5.1-5.7		4.8-5.7		
August		7.3-7.6		6.5-7.8		
Saxifraga bronchialis						
May		1.2-1.5	1.2-1.5	———	———	———
June		3.3-3.6	2.8-3.6	3.4-3.9	2.8-3.5	2.4-2.6
July		3.7-4.1	3.7-4.2	3.6-3.9	3.4-3.9	3.2-4.1
August		7.1-7.4	7.1-7.6	6.8-7.1	6.6-6.9	6.6-7.2
Silene acaulis						
May			1.0-1.0		———	———
June			3.1-3.8		2.2-3.1	2.9-3.4
July			5.1-5.3		4.3-4.7	3.1-3.6
August			6.9-7.5		6.5-7.3	7.1-7.3
Dryas octopetala						
May			1.0-1.0		———	———
June			2.1-2.8		1.7-2.5	1.3-2.1
July			5.1-5.8		3.8-4.4	3.2-3.9
August			7.3-7.5		7.1-7.6	7.1-7.5

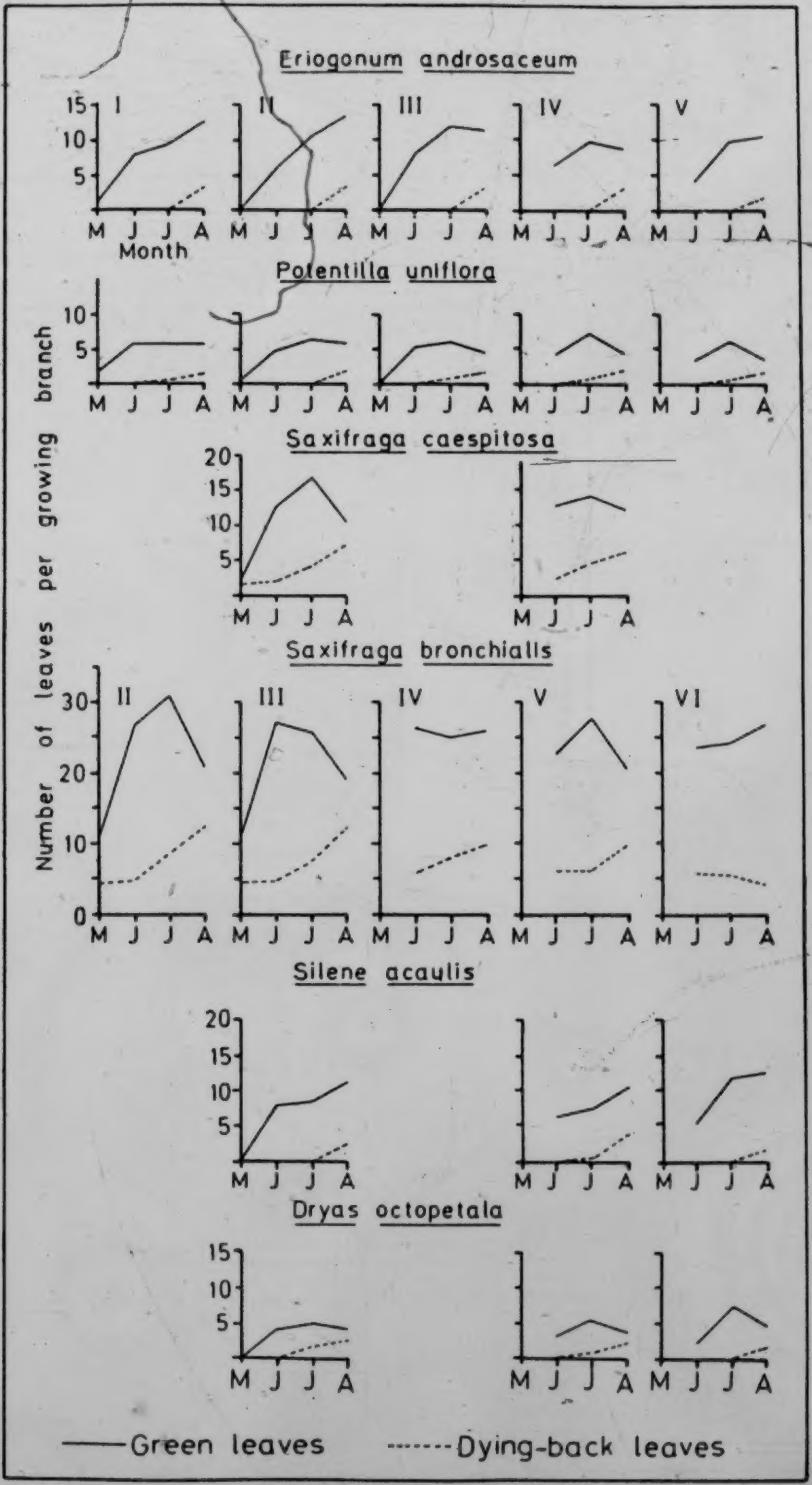
after about 10 weeks from the first leaf appearance. The time period required for the various phases tended to be rather stable within the species. The time of initiation for particular phases varied considerably from site to site and to a greater degree among different species at a given site (Table 3.3).

All the species investigated showed rapid growth of foliage at the beginning of the growing season. During late July / early August, the rate of leaf production slowed down and flowering and fruiting rates increased (Figure 3.1). *E. androsaceum* and *S. bronchialis* showed a lag time between the phases of leaf expansion and floral bud development. These two species reached their flowering stage more than six weeks after the onset of leaf elongation. The lag time may be related to the depletion of reserves from the last growing season. *P. uniflora* and *S. caespitosa* reached the flowering stage ahead of the other species, except for *S. acaulis* and *D. octopetala* on site III. These species took about five to six weeks to develop from the appearance of new leaves to the open flowers.

All plants produced leaves continuously through the growing season. Leaf production decreased towards the end of the growing season (Figure 3.2). Thus, fruit development occurred when there was little allocation to leaf expansion. In most species, the number of green leaves per shoot reached a maximum during midsummer. The average number of leaves per shoot produced by *Eriogonum androsaceum* was 12, while the average yearly production of leaves per shoot in *Potentilla uniflora* was 6 leaves. *Saxifraga caespitosa* produced 14 new leaves per shoot on average during the growing season. The yearly production of leaves per shoot in *Saxifraga bronchialis* was high, up to 22 leaves. For *Silene acaulis*, the average annual growth amounted to 12 leaves per shoot, while in *Dryas octopetala* the number of leaves produced on the main shoot apex was 4 leaves. In some of the species (*E. androsaceum, P. uniflora*) additional leaves were initiated in late summer from buds in the current year leaf axile. This is considered a second leaf flushing (multiple leafing), which compensates for the high rates of leaf die-back towards the end of the growing season.

Leaf death (die-back) in the different species occurred at different times of the season (Figure 3.2), regardless of site variation. The rate of leaf die-back reached a peak by the end of the growing season, with the exception of *S. bronchialis* on the NE side, where it attained the highest rate of leaf die-back early in the growing season. In the two winter-green *Saxifraga* species, leaf die-back started with the beginning of the growing season. The leaves of *S. bronchialis* may function for two growing seasons, as they pass the winter in a green state, and wither in the course of the succeeding summer and second winter. The plants retain from 30 to 50% of their photosynthetic green leaves over the winter.

Figure (3.2): Number of green leaves and dying-back leaves per branch of the studied species at various sites in May, June, July and August 1984. Sample size: Five branches per individual. 30 individuals from each species per site. For Standard Deviation see Appendix (4).


Eriogonum androsaceum
I
II
III
IV
V
15
10
5
M J J A
Month
Potentilla uniflora
10
5
Saxifraga caespitosa
20
15
10
5
Saxifraga bronchialis
II
III
IV
V
VI
30
20
10
0
Number of leaves per growing branch
Silene acaulis
20
15
10
5
Dryas octopetala
15
10
5
M J J A
Green leaves
Dying-back leaves

In *S. caespitosa*, only the leaves last developed (from 20 to 30% of its green leaves) persist during the winter, but they wither as early as the beginning of the succeeding growing season. However, in the two species of *Saxifraga*, overwintering leaves contributed an important fraction of total leaves early in the season. In all species, the dead leaves remain on the shoot for many years, buffering and protecting the internal plant microenvironment against temperature and moisture fluctuations.

In all study sites, the average number of flowering stalks increases almost linearly with the size of the cushion plant (Figure 3.3; Appendix 5). This holds true for all species investigated. Flowering seems to be more synchronous and occurs over a period of 2 to 3 weeks. The difference between sites in number of flowering stalks per individual plant was variable and species-dependent (table 3.4). Generally, the number of flowering stalks per individual plant decreased with elevation. The plants on the NE side (site VI) produced fewer flowers than plants on the SW side, with the exception of *D. octopetala*, which produced more flowers per square meter of plant surface area on the NE side. The data in Table (3.5) indicate that the completion of a phenological cycle needs two growing seasons, at least when the growing conditions are poor. 15 to 43% of the individual plants (all species included) did not flower, in spite of luxuriant vegetation growth.

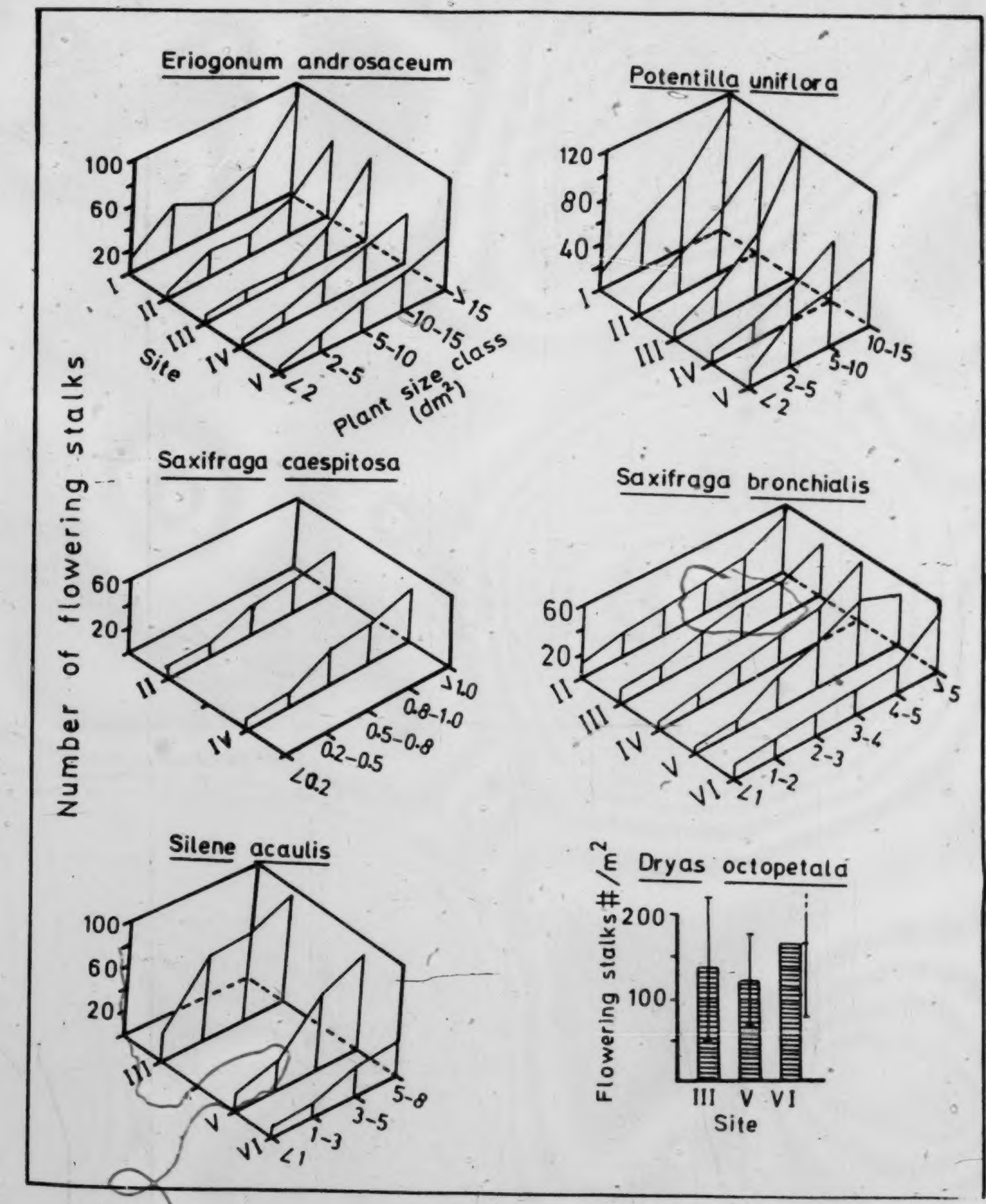


Figure (3.3): Number of flowering stalks produced per individual plant of the studied species at various sites during the growing season of 1984, Table (3.4) The range of variability in numbers of flowering stalks produced per individual plant at various sites during the growing season of 1984. * number per m^2 of plant carpets.

Species	Site					
(Size class dm^2)	I	II	III	IV	V	VI
Eriogonum androsaceum						
<2	008–024	004–011	002–015	004–013	003–008	
2-5	013–072	010–037	007–018	007–020	006–023	
5-10	015–044	010–032	003–022	005–042	015–030	
10-15	030–051	025–041	025–038	027–046	026–039	
>15	052–110	040–106	040–120	005–088	010–083	
Potentiall uniflora						
<2	010–025	012–026	006–015	007–017	009–019	
2-5	028–060	028–051	007–045	009–030	022–057	
5-10	028–125	035–069	049–068	025–036	039–068	
10-15	065–156	062–120	075–167	033–072	048–070	
Saxifraga caespitosa						
<0.2		005–016		005–013		
0.2-0.5		007–018		009–023		
0.5-0.8		015–032		025–031		
0.8-1.0		019–036		025–040		
>1.0		023–048		031–052		
Saxifraga bronchialis						
<1		010–019	007–023	006–010	005–012	008–022
1-2		009–030	012–019	009–019	005–024	010–020
2-3		015–032	023–030	012–026	021–035	013–026
3-4		021–038	023–041	017–036	033–051	015–028
4-5		021–045	025–044	025–038	045–066	019–031
>5		042–058	040–057	044–065	031–065	042–057
Silene acaulis						
1			014–030		010–027	007–013
1-3			038–106		010–044	008–019
3-5			062–098		036–093	017–028
5-8			066–124		061–110	024–036
*Dryas octopetala**			053–220		050–186	062–272

Table (3.5): Percentage of individuals per species which failed to produce flowers during the growing season of 1984. Observations were made during August 1984 in 10 random quadrats (5 x 5 m) per site. Number of individual plants observed in brackets.

Species	Study sites					
	I	II	III	IV	V	VI
Eriogonum androsaceum	20(73)	32(62)	33(65)	30(48)	38(44)	
Potentilla uniflora	18(68)	26(55)	38(71)	35(62)	43(57)	
Saxifraga caespitosa		25(26)		20(18)		
Saxifraga bronchialis		22(34)	28(61)	26(20)	30(45)	32(48)
Silene acaulis			15(32)		18(46)	20(41)
Dryas octopetala			?		?	?

D. Discussion

Plant phenology can often be helpful in describing microenvironmental differences between various habitats (Bliss 1962, Jackson 1966), as well as along environmental gradients (Ladygina 1960, Douglas and Bliss 1977). The phenological patterns of cushion plants on Mt. Allan seem to be governed by two main factors: 1) The availability of moisture from thawing snow in spring and early summer; and 2) the short growing season.

The high soil moisture content during and immediately after the snow melt initiated leaf production in all investigated species on all sites. This was in spite of cool temperatures. None of the observed species opened its flower buds soon after snow melt, as has been reported for *Ranunculus glacialis* by Moser et al. (1977). Only after considerable time was spent on the development of vegetative tissue (five to seven weeks) was the flowering stage reached. Differences in site conditions did not alter this pattern. Rather, the observed plants followed their endogenous rhythm for the process of reproductive development. (Many individuals of *Silene acaulis* at the crest site did, however, open their flowers first on the SE-side of the cushion). Seed setting and senescence of summergreen leaves were synchronous in different species and at different sites, regardless of the time of emergence from under the snow and sprouting.

McGraw et al. (1983) explained the early senescence of tundra plants by cold overall temperatures. But in the present study, low temperatures do not seem to be the operative cue for the onset of early senescence. Even in late summer, temperatures on Mt. Allan were still high. The increasing water stress at that time may be seen as a more convincing trigger for senescence. However, the decrease in soil moisture certainly did not have such uniform timing. The behavior of the plants must therefore be understood as following an endogenous rhythm.

Moser (1968), Larcher (1980), Walter (1985) described this phenomenon. The leaves of summergreen high mountain plants in the European Alps turn yellow and brown by the end of August, which is usually about two weeks before the onset of severe fall frosts. The advantage of this mechanism can be understood as follows. Since all of the observed plants are perennials, their success is not founded on completion of a full life cycle within one growing season. Soerensen (1941), Holway and Ward (1965), Mark (1968), and many other authors have shown that in arctic and alpine plants, flower primordia are often produced one or more years before flowering occurs. For the survival of the plant it is much more important that all available assimilates are translocated to the safe underground organs in time, than to risk a complete loss after a single severe night frost in early fall. This way, the chances for success in next year's reproduction are increased, even if time may run short for this year's seed maturation. This conclusion is supported further by the fact that older cushion plants produce relatively more flowers than younger ones (Fig 3.3), indicating a strategy of longevity (Pianka 1983): Priority is given to the accumulation of phytomass; sexual reproduction comes second.

Some flexibility may exist in the genetic fixation of such behavior. The timing and duration of phenophases were quite different among the individuals of *E. androsaceum* or *P. uniflora*, depending on altitude and site. On sites at higher elevations, vegetative growth started about one to two weeks later than at the lowest site, reducing the phenological cycle to about ten weeks. In spite of this difference in time and in microenvironmental conditions, fruiting occurred at almost the same time over the entire altitudinal range (from 2100 m to 2360 m asl). Ladygina (1960), Clarke (1968) and Billings (1974) described this phenomenon for other alpine plants and attribute it to the "different intensity" of physiological events taking place at different altitudes. For this study, a more likely conclusion is that seeds produced at different altitudes reached different grades of maturity. Seeds from 2360 m may not be as viable or may be not viable at all.

Both *E. androsaceum* and *P. uniflora* are adapted through the timing of phenological events according to the environmental conditions, except for the termination of the cycle. This flexibility may account for their local relatively wide range of distribution (Hoffmann and Walker 1980). In contrast, *S. caespitosa* individuals showed no apparent differences in phenophase development. This could account for its rather local restricted range of distribution.

Evergreen and summergreen cushion plants did not differ fundamentally in their phenological pattern. The wintergreen *Saxifraga* species did not flower earlier, despite the fact that they are able to compensate for low photosynthetic rates by an early beginning of growth (Chabot and Hicks 1982). *Dryas octopetala* has been reported to be wintergreen (Soerensen 1941, Murray and Miller 1982). This study cannot confirm the evergreen property, as all fully developed leaves wither by the end of autumn and during the winter. According to Chabot and Hicks (1982), the summergreen strategy reduces the surface area for transpiration and conserves moisture for perennating tissues.

E. Summary and Conclusions

Six sampling sites with differences in elevation, slope, aspect and vegetation cover were established in the study area on Mt. Allan. Phenological observations were made in May, June, July and August 1984 on six cushion plant species. The following results were obtained:

1. The timing of phenological events in alpine cushion plants differed more between species than within species at different sites.

2. Plants on sites at lower elevations on the SW side developed more rapidly than plants at high elevations and plants on the NE side.
3. Fast sprouting occurs after the onset of spring. It is achieved by the differentiation of vegetative buds during the previous growing season.
4. Regardless of site variation and species, a pronounced shoot die-back (senescence) coincided with the onset of seed set in late summer.
5. The observed summer senescence and the truncated activity of cushion plants is controlled by genetic makeup rather than by cold temperatures.
6. The average number of leaves produced during the growing season reached from 4 in *D. octopetala* to as many as 22 in *S. bronchialis*. In some species, additional leaves were initiated in late summer from buds in the current leaf axile (multiple leafing). Such species may utilize favourable periods in fall.
7. The widely distributed species are able to modify their phenological behavior to cope with the environmental limitations.

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IV. Rooting Patterns

A. Introduction

Roots and root growth have received relatively little attention in analyses of ecosystems at all latitudes (Shaver and Billings 1975). The root systems of only a few alpine cushion plants are described in the literature. These descriptions show a lack of common patterns in the rooting characteristics. In contrast, the aboveground structure has shown a distinct physiognomy in different parts of the world, although some variation exists between species in the particular mode of growth (Rauh 1939).

The compact form of the aboveground portions of cushion plants is conspicuously adapted to some conditions of the alpine environment. One might suspect that the less evident subterranean organs of these plants would also possess structural characteristics with particular advantages, as each unit of the aboveground tissue requires a larger amount of root surface than might be the case under more favourable conditions.

Some aspects of a few cushion plant root systems have been presented elsewhere (Hauri 1913, Jessen 1913, Schroeter 1926, Daubenmire 1941, Holch et al. 1941, Griggs 1956, Jones and Richards 1962, Elkington 1971, Jochimsen 1983). However, the belowground phenomena in the alpine tundra still remain poorly understood and there is a need for continued studies (Bliss 1971, Weber and May 1977). Jochimsen (1983) observed that at several sites which differed mainly in grain size and water supply, soil movement not only influenced the position of roots of pioneer plants within the soil, but also their ramification. The degree of stabilization achieved depends on the configuration, density and strength of the root system.

In an ecosystem where the primary producers have problems in obtaining energy, one might expect conservation of energy and matter expenditures for the production of various organs. Carbon partitioning determines the functional equilibrium between root and shoot, which in turn determines the life form (Schulze 1983). Species with similar life forms or life cycles tend to have similar root/shoot ratios, and their occurrence is related to parameters of the physical environment (Smith and Klinger 1985).

Because of the accumulation of dead plant organs, particularly leaves, within the mature cushion plant, a slow turnover takes place relative to the life span of the plant. The cushion holds a store of water which is available to the plant, and the substratum remains distinctly moist during water stress periods (Rauh 1939, Jones and Richards 1982). Apart from the adaptive implications of litter accumulation in terms of water storage and nutrient recycling, the litter improves the structure of the immature rocky soil and creates diverse microsites which supports the rooting pattern.

The objectives of this chapter are: 1) to describe the nature of underground parts of six cushion plants and to find out the extent of variation in root characters as affected by topography among four sites, and the mechanical impedance offered by alpine rocky soils; 2) to describe the pattern and quantity of dry matter partitioning into plant organs, as well as the phytomass ratio of live to dead shoots; and 3) to interpret the ecological significance of these findings.

The field work was conducted in the summer of 1983 during the flowering peak of plants.

B. Materials and Methods

In order to examine the relationship between root development and dry matter components of each of the six species and differences in topography and aspect, four sites were selected on the southwest side (lower slope and ridge), the upper crest, and the northeast slope of Mt. Allan (see Chapter I, Figure 1.1).

The root systems were excavated manually. Field measurements and sketches were made of the extent of the plants aboveground, and the underground systems were carefully traced, measured and drawn to scale on graph paper. Roots less than about 1mm in diameter were too small to be traced in the soil for distances greater than a few centimeters. But these small roots generally appeared to comprise only a small percentage of the total length of the root systems and were confined to the ends of the larger roots.

The roots were separated from the shoots and the aboveground portion was sorted into stem, leaf, flower and dead organic matter (loose and attached litter) components. Materials were oven-dried for 48 hours at 80°C at the Kananaskis Research Centre before weighing.

For detailed excavation, three plants of the same species and of similar size were selected at each site. In a few instances, the abundance of rocks and gravel in the soil prevented excavation to depths sufficient to reach the maximum depth of the roots, because the roots disappeared into cracks of solid rocks. Therefore, in addition to the harvested plants, other specimens of similar size were partially excavated to find the general type of root system of the species, thus doing less damage to the plants. In every case the root system which appeared most typical to the site was selected for illustration.

Other information were recorded for every site included descriptions of the soil profiles. Three ratios were calculated: Radial root spread/shoot size ratio, root/shoot ratio (for living material), and dead/live shoot ratio. Live and dead root and shoot material were separated visually. Live roots and stems were distinguished from darker brown fragile dead roots and stems by their lighter colour and strength when stretched. Leaves with autumn or green colouration were considered live. Methods of measuring litter fall have not been standardized. Consequently, some variation may result from variation in methods. Such variations are probably small in the case of cushion plants, because most organic matter is kept within the bulk of the plant.

C. Results

Root Morphology

The root systems of the six species studied have different characters. Measurements of the root systems are summarized in Table (4.1). Their profiles are presented in Figure (4.1). The same species exhibit different types of root growth in different habitats. In all species, feeder roots arise from the old stems and proliferate in the internal packing material, remaining restricted to the body of the cushion plant. Many roots extend from decumbent stems under the base of the cushion plant, producing adventitious roots at varying intervals.

Potentilla uniflora

The plant forms a large cushion characterized by firmness and compactness.

At the lower slope site (SW side), the root system is deeply penetrating (Figure 4.1) and growing to a depth of 4.5 dm below the ground surface. The main root is ramified and bifurcated at different levels, giving numerous laterals which grow in all directions from the plant. Many fine feeder roots grow from roots of all sizes and at varying intervals. In top view, plants are able to extend their root area in all directions to about 43.8 dm^2. The plant drawn was dense, circular and approximately 10.2 dm^3 in volume.

The root systems of plants at the ridge site (SW side) have prominent "tap" roots and are commonly found from the cushion leading up the slope. Their roots frequently change direction, with the thinner ends more or less fixed in deep soil. This pattern is probably in response to the rocky soil. The main root is sparsely branched and confined mainly to spaces between shallow, broken rock fragments and crevices. It extends downward a maximum of only 2.3 dm, and attains the highest radial root spread of all species studied. Many adventitious roots arise from the prostrate branches and grow in all directions. The plant drawn was oval in shape and approximately 16.6 dm^3 in volume.

At the crest site, the root depth below the surface is quite uniform and follows the surface topography closely. Roots did not penetrate downward more than 2.3 dm, and extended laterally 15.1 dm. The plant drawn was approximately circular and its volume was 3.8 dm^3.

Eriogonum androsaceum

The root sytems of excavated plants at all sites closely resemble those of *Potentilla uniflora* except at the ridge site, where the roots are more or less fixed beneath the broken rock fragments subject to movement. The slippage of rock fragments and gravel soil had drawn the root system tight and nearly straight and it extended uphill. Because of strong wind erosion, some parts of the main roots were exposed or were very shallow. Adventitious root buds arise and sprout from these exposed roots, and a new plant originates when the connection with the original plant decays. A cluster of rootlets develops from the main root under the base of the newly formed plant. The root buds are mostly initiated on severed or damaged roots (Steeves and Sussex 1972). Shoot meristems are developed from cells of internal tissue.

Saxifraga caespitosa

This species lives on the most exposed ridges, where it finds some shelter in holes between rocks. It branches profusely to form a densely caespitose leafy cushion. Mature plants form loose delicate cushions. The underground parts are correspondingly poorly developed (Figure 4.1). The onesided main tap root system again lies uphill, indicating soil movement. Feeble branched lateral roots penetrate to a depth of 1.3 dm. The plant drawn was nearly hemispherical and 0.8 dm^3 in size.

Saxifraga bronchialis

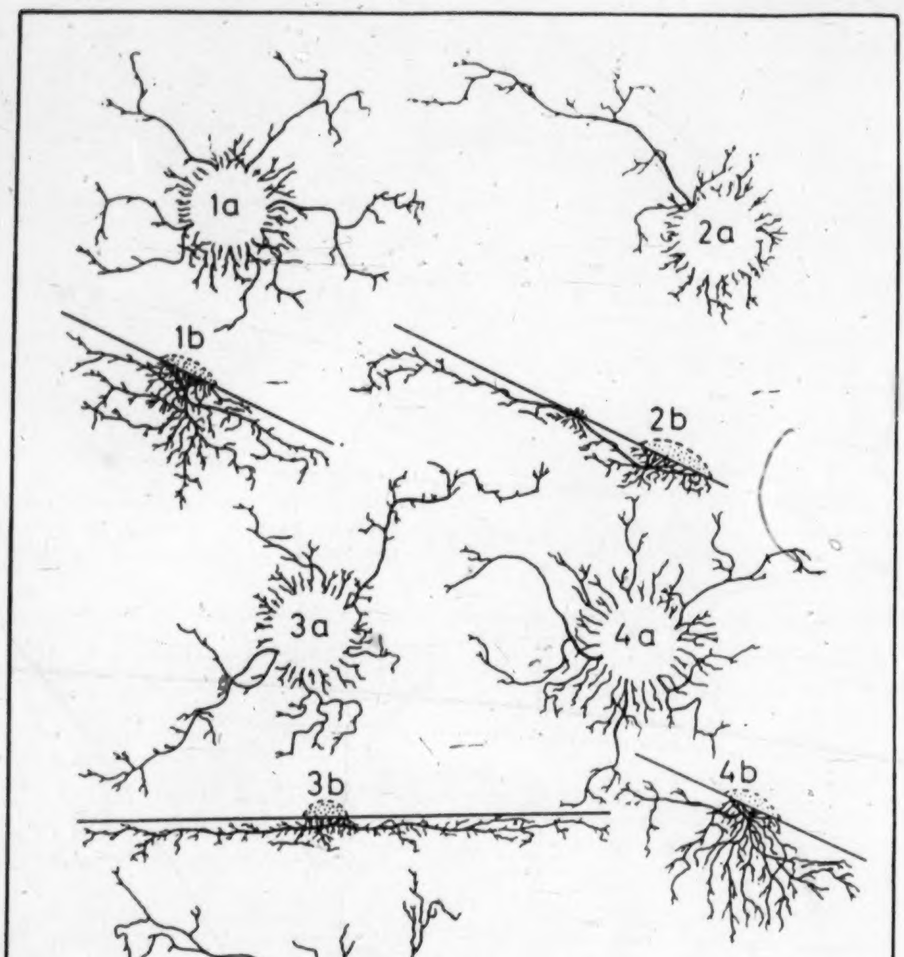
At the NE slope, the root system of this species consisted of a disorderly, mixed mass of root branches which spread in all directions as they elongated. With age, the prostrate branches become rooted. The shoots radiate obliquely upward to produce what appears superficially to be a colony of separate plants, so that each may develop a more or less independent root system.

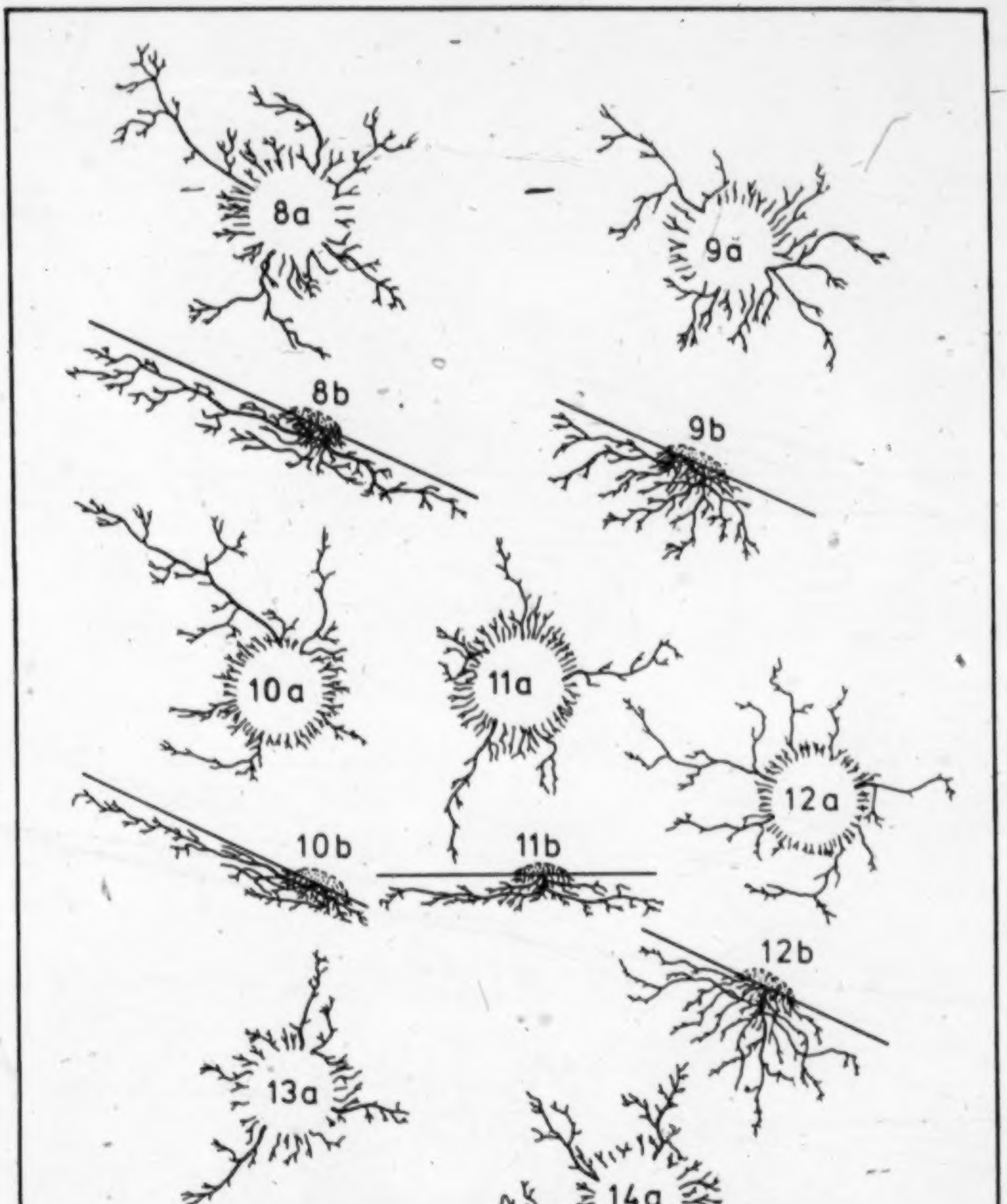
The maximum depth of root penetration of plants growing at the ridge site (SW side) is shallower than that of the plants on the NE side. In contrast, the maximum radial root spread is greatest in plants at the ridge site. The root systems seem largely conditioned by soil constitution and soil pockets between stones which help in providing the plants with water. The soil is quite stable; no downhill movement of the cushions is indicated by the root system.

Silene acaulis

It is a dense round pancake of a plant, spreading radially on the ground or bulging up into a flat dome, supported by a long and strong, but much branched tap root or a cluster of "tap" roots (Figure 4.1). The root system of the excavated plants at the NE slope is characterized by a ramified main root, which bifurcates at different levels, yielding numerous laterals. From the lower surface of prostrate branches adventitious roots arise, which augment the primary root system. The live roots were light yellow in colour, penetrated to 4.4 dm and extend horizontally approximately by twice as much as root depth.

Figure (4.1): Root system sketches of the studied species at various sites of the study area: a - Radial root spread (top view). b - Vertical root depth (side view). 1, 2, 3 - *Eriogonum androsaceum* at the lower slope, ridge and crest, respectively. 4, 5, 6 - *Potentilla uniflora* at the lower slope, ridge and crest. 7 - *Saxifraga caespitosa* at the ridge. 8, 9 - *Saxifraga bronchialis* at the ridge and NE slope. 10, 11, 12 - *Silene acaulis* at the ridge, crest, and NE slope. 13, 14 - *Dryas octopetala* at the crest and NE slope.


1a
2a
1b
2b
3a
4a
3b
4b
5a
6a
5b
6b
7a
7b
50 cm
Crest


8a
9a
8b
9b
Crest
50 cm

The plant drawn was circular and about 3.2 dm^3 in size.

At the ridge site (SW side), excavations were made in this species' typical habitat of rocky soil. The root follows the slope upward to depths of 1.0 dm below the surface. The slippage of soil accounts for this one-sided root pattern. The plant drawn was oval in shape and about 2.5 dm^3 in size.

At the crest, the root systems fail to show the one-sided extension of roots as well as the deep penetration when compared with those at the other two sites. The radial root spread and the horizontal root extension far exceeded the root penetration. The plant drawn was circular in shape and about 2.9 dm^3 in size.

Dryas octopetala

The twisted, woody stems of this species trail along the ground surface, forming a thick assemblage of shoots barely close enough to each other to deserve the name of cushion plant. However, as the spaces between the shoots are filled with substrate material, it can be termed after Hauri (1913) as a loose cushion plant at least in its early stages.

At both sites (the crest and the NE slope), plants have a stout, woody root-stock, branching below and often penetrating into rocky crevices. From these strongly developed subterranean horizontal systems (rhizome and root systems), many stem branches arise upward, forming shoots which grow to the surface. These subterranean systems gave rise to smaller roots, penetrate the upper 1.7 dm of the soil and extended laterally to 9.8 dm. Plants extending over many square decimeters of surface may have a common underground system. Older woody stems often bear adventitious roots on the underside.

Root/Shoot Ratios

The ratios for radial root spread/shoot size and dry weight of live root/shoot parts are compared for the six species in Table (4.1). The radial root spread/shoot size ratios in all species studied at different sites show a wide range of variation and are greater than unity. The highest ratio is 22.4 in *Saxifraga caespitosa* and the lowest ratio averages 1.2 in *Dryas octopetala* at the crest site.

The dry phytomass root/shoot ratios differ slightly among species from various sites. The extremes are attained by *Saxifraga bronchialis* at the ridge (0.34) and *Silene acaulis* at the NE slope (1.17). The majority exhibits a ratio of less than unity.

Litter Accumulation

The cushion plant packing material includes a great variety of substances. It is derived in part from the litter of the plant itself and in part from inorganic matter varying from fine sand to fairly large stones overgrown or brought in by wind, snow fall, earth-falls, rain, etc.

Table (4.1): Root and shoot characteristics of the studied species at various sites of the study area. (Standard deviation in brackets). n=3

Species (character)	South-west side		Upper crest	North-east slope
	Lower slope	Ridge		
Eriogonum androsaceum				
1-shoot size (sq.dm)	08.00(1.3)	18.10(5.2)	05.30(0.4)	
2-root depth (dm)	04.40(0.5)	02.00(0.3)	01.50(0.3)	
3-horizontal root extension (dm)	10.30(2.4)	13.80(3.6)	18.50(1.8)	
4-radial root spread (sq.dm)	42.40(5.1)	23.40(3.7)	40.20(1.2)	
5-root spread/shoot size ratio	05.30(—)	01.30(—)	07.60(—)	
6-live shoot dry phytomass (g)	12.00(2.7)	15.60(4.5)	10.50(2.8)	
7-live root dry phytomass (g)	07.90(1.5)	15.80(2.0)	09.00(1.8)	
8-root/shoot ratio	00.66(—)	01.01(—)	00.86(—)	
9-dry litter phytomass (g)	32.30(6.8)	58.00(9.3)	30.50(6.5)	
10-dead/live shoot ratio	02.69(—)	03.72(—)	02.91(—)	
Potentialla uniflora				
1-shoot size (sq.dm)	10.20(2.8)	16.60(4.1)	03.90(1.2)	
2-root depth (dm)	04.50(0.8)	02.30(0.5)	02.30(0.5)	
3-horizontal root extension (dm)	09.80(1.5)	12.50(2.4)	15.10(2.8)	
4-radial root spread (sq.dm)	43.80(6.3)	52.00(8.2)	44.60(2.6)	
5-root spread/shoot size ratio	04.30(—)	03.10(—)	11.70(—)	
6-live shoot dry phytomass (g)	17.50(3.7)	19.30(4.5)	11.50(2.4)	
7-live root dry phytomass (g)	10.80(1.3)	09.50(2.1)	04.20(1.3)	
8-root/shoot ratio	00.62(—)	00.49(—)	00.37(—)	
9-dry litter phytomass (g)	35.40(5.7)	36.30(4.7)	25.80(3.6)	
10-dead/live shoot ratio	02.02(—)	01.88(—)	02.24(—)	
Saxifraga caespitosa				
1-shoot size (sq.dm)		00.80(0.2)		
2-root depth (dm)		01.30(0.2)		
3-horizontal root extension (dm)		04.90(0.5)		
4-radial root spread (sq.dm)		17.80(1.6)		
5-root spread/shoot size ratio		22.40(—)		
6-live shoot dry phytomass (g)		02.50(0.5)		
7-live root dry phytomass (g)		01.10(0.2)		
8-root/shoot ratio		00.44(—)		
9-dry litter phytomass (g)		03.10(0.5)		
10-dead/live shoot ratio		01.24(—)		

(cont'd next page)

Table (4.1): Cont.

Species (character)	South-west side Lower slope	South-west side Ridge	Upper crest	North-east slope
saxifraga bronchialis				
1-shoot size (sq.dm)		02.00(0.6)		03.20(1.0)
2-root depth (dm)		02.00(0.5)		03.00(0.8)
3-horizontal root extension (dm)		12.70(1.9)		07.40(0.8)
4-radial root spread (sq.dm)		34.00(3.2)		23.30(2.6)
5-root spread/shoot size ratio		17.00(—)		07.30(---)
6-live shoot dry phytomass (g)		03.50(1.0)		04.10(1.2)
7-live root dry phytomass (g)		01.20(0.3)		01.50(0.5)
8-root/shoot ratio		00.34(—)		00.37(---)
9-dry litter phytomass (g)		06.70(1.3)		08.70(2.0)
10-dead/live shoot ratio		01.91(—)		02.12(---)
Silene acaulis				
1-shoot size (sq.dm)		02.50(0.8)	02.90(1.0)	03.20(1.1)
2-root depth (dm)		01.00(0.2)	01.50(0.2)	04.40(1.3)
3-horizontal root extension (dm)		11.80(1.7)	08.30(1.2)	08.30(2.5)
4-radial root spread (sq.dm)		21.80(2.3)	21.70(3.1)	26.40(3.4)
5-root spread/shoot size ratio		08.70(—)	07.50(—)	08.30(---)
6-live shoot dry phytomass (g)		09.20(2.1)	06.30(1.3)	10.40(1.8)
7-live root dry phytomass (g)		07.30(1.5)	06.10(1.3)	12.20(2.4)
8-root/shoot ratio		00.79(—)	00.97(—)	01.17(---)
9-dry litter phytomass (g)		09.80(1.8)	08.30(1.1)	14.20(1.5)
10-dead/live shoot ratio		01.07(—)	01.32(—)	01.37(---)
Dryas octopetala				
1-shoot size (sq.dm)			16.60(1.5)	21.20(2.7)
2-root depth (dm)			01.30(0.2)	01.70(0.4)
3-horizontal root extension (dm)			09.60(2.1)	09.80(1.4)
4-radial root spread (sq.dm)			19.70(1.7)	38.30(2.8)
5-root spread/shoot size ratio			01.20(—)	01.80(---)
6-live shoot dry phytomass (g)			20.00(3.2)	35.30(4.5)
7-live root dry phytomass (g)			11.70(2.6)	17.10(3.8)
8-root/shoot ratio			00.59(—)	00.48(---)
9-dry litter phytomass (g)			12.50(1.5)	35.80(3.6)
10-dead/live shoot ratio			00.63(---)	01.01(---)

In this study the accumulated litter of the plant was separated and estimated. The ratios of standing dead/live shoot (D/L ratios) are fairly high and vary between 0.63 in *Dryas* (at the crest) and 3.72 in *Eriogonum* at the ridge (SW). ~~The~~ D/L ratio exceeds 1:00 in all species studied except for *Dryas* at the crest (0.63). The absolute amounts of accumulated litter varied within the same species at different sites. The litter phytomass is larger in old plants (because of their larger size).

D. Discussion

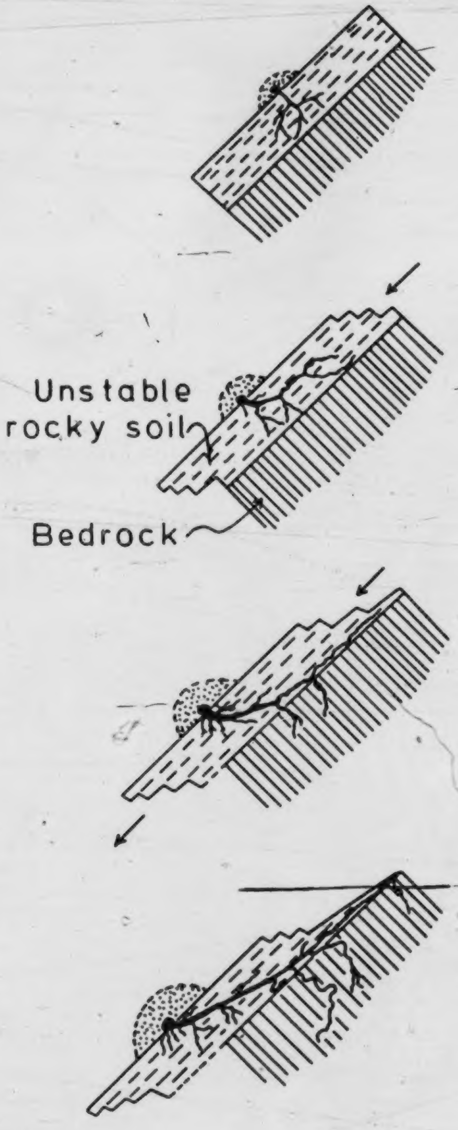
Many seed plants in exposed positions with little or no soil accumulation are xerophytes (Cox 1933, Holch et al. 1941, and Griggs 1956). Alpine cushion plants grow in these exposed locations. Their reduced aerial and extensive subterranean structures are typical for the alpine and other extreme environments. There is a site-dependent change of length, depth and root configuration in alpine cushion plants. Local conditions obviously control the rooting pattern.

The species studied showed extensively developed root systems. The plants sometimes anchor themselves by deep roots extending a considerable distance downward into the more stable material below or into fractured rock, and have rather temporary but extensive root development in the superficial layer of less stable rock waste. The pattern of root systems seems to have a large range of adaptation to variable scil conditions, that is, they have sufficient plasticity to adjust to mechanical soil impedance (stress) in such gravel-slide habitats. According to Briggs and Walters (1984) and Grime et al.(1986), the root and shoot morphological plasticity maintains the functional efficiency of plants. Such plasticity is regarded as a mechanism compensating for the lack of locomotion in plants and supplementing the role of genetic variation as a determinant of wide ecological amplitude and persistence in fluctuating conditions.

Two classic studies carried out by Daubenmire (1941) and Holch et al. (1941) on root systems of alpine plants show some discrepancies about root depth and configuration. Daubenmire examined the subterranean structural characteristics of 16 cushion and mat plant species and concluded that there are no striking consistantly occurring subterranean adaptations to the alpine environment. Holch et al. (1941) however pointed out that alpine plants are peculiar in their growth habits both above and below ground, and are well adapted to the alpine environment through site-dependent root plasticity and high root/shoot ratio.

The data of this study suggest the following: At lower slopes on Mount Allan, where the soil is more stable, plants have strong, deeply penetrating roots and are able to extend their root area in all directions. Their root systems are much-branched and fairly wide spreading. The roots show great density resulting from secondary and tertiary ramification. Therefore, better utilization of soil water is possible.

Cannon (1949) reported that "specialized" root systems are those with all of the roots relatively close to the surface of the substratum. Also, he found that primary roots are positively geotropic, while adventitious roots are more strongly influenced by other environmental factors (also Bliss 1956, Bell and Bliss 1978). At the ridge site, the bulk of the roots of most species followed the slope upward, giving the impression of negative geotropism. But this rooting pattern results from soil movement (Cruden 1985). As the cushions are slowly transported downhill when the surface of the soil is moving, the tap roots, firmly anchored in crevices of the parent material, are stretched and eventually show the typical "uphill" configuration (Fig.4.2). So, the root interaction with the mechanical impedance of the rocky soil greatly affects the root configuration (Hsiao 1973, Gorchakovskii and Matyashenko 1978). However, the mechanism for regulating the effects of mechanical impedance on root development is not known (Feldman 1984). Cushion plants growing at the ridges on unstable rocky soil mat their roots in the finer and moister ground below the creeping masses of loose rock and gravel. On the ridges and steep slopes, the combination of the one-sided root system with the spherical or flat shape of the shoot gives the impression that cushion plants are like comets or kites flying down the mountain.



Positive geotropic growth of root in early stages.

Due to surface rocky soil movement, roots freguently change direction, configuration and position.

As a result of soil movement, the root system becomes one-sided and grows up slope direction.

Figure (4.2): Hypothetical development of one-sided root configuration.

Mapping of the major roots in top view showed extensive radial roots, spreading far beyond the range of the corresponding shoots. The radial root spread/shoot size ratios were greater than unity in all species. Such extensive radial root spreading is considered as an adaptation of these "pioneer" plants to conditions on gravel slides and dry slopes. The ecological significance of such extensive root development is that plants extend their root area and are thus better fitted to secure water when the soil is moistened. Also, the gravelly soil within a large area is held more or less firmly in place. The magnitude of aboveground versus belowground phytomass is attributed by Webber and May (1977) to species characteristics and growth form rather than to the environment. In contrast, Smith and Klinger (1985) found that it is related to parameters of the physical environment. This study shows that the root/shoot ratio is basically a function of the species and growth form, but the local environment causes some modifications. There were differences in the ratios among sites within the same species. Surprisingly, species of similar distribution exhibited the same trend of variation of radial root spread/shoot size ratio, for example *Potentilla* and *Eriogonum* showing the highest ratios at the crest site and the lowest ratios at the ridge site (SW side), while *Saxifraga bronchialis* and *Silene acaulis* have their highest ratios at the ridge site. In the majority of cases the ratios were less than unity, which is in line with Bliss and

Mark (1974), who found that an unusually large proportion of the total standing crop is aboveground. This can be attributed to low rates of turnover of aboveground biomass (Webber and May 1977). Bray (1963) pointed out that root production decreases with age, and Monk (1966) has shown that dry weights of roots and shoots were found to be significantly correlated with height. So, tne possible decrease in root/shoot ratio with age may be associated with an increase in the non-living aboveground litter, forming the packing material of cushion plants.

In comparison with other studies, the root/shoot ratios vary considerably for alpine cushion plants. Dennis and Johnson (1970), Bliss and Mark (1974), Webber and May (1977) have reported root/shoot ratios for cushion plants similar to the results of this study. However, in drier sites on Mt. Allan, there is a larger aboveground standing crop. Wielgolaski (1972) reported an increase in root/shoot ratios for non-cushion plants along a moisture gradient. Scott and Billings (1964), and also Billings (1974) found the root/shoot ratio of non-cushion plants to be larger in moist areas than on relatively dry sites. However, experimental studies on plant growth forms by Penka (1965) showed that the root/shoot ratio for irrigated and non-irrigated plants was substantially the same.

The results show that litter accumulation by cushion plants varies considerably within the same species, and between species at different sites. Also, the observed pattern of high standing dead/live shoot ratios may be accountable to low microbial activity. In agreement with Bliss and Svoboda (1984) and Bliss et al. (1984) litter accumulation by cushion plants represents a major fraction of its standing crop and contributes a substantial part of the total organic carbon on alpine sites. This can be attributed to both climatic and edaphic factors (Jordan 1971, Meentemeyer et al. 1982). The accumulation of organic matter can be viewed as an adaptive mechanism in different ways. 1. It supports the process of adventitious rooting, since all the stem parts are buried in or under the packing material of the cushion plant. 2. The accumulated litter remains for most of the plant life protecting the growing points and buffering the internal clump environment against temperature and moisture fluctuations (Svoboda 1973 and 1977). 3. Cushion plants take advantage of the less fluctuating and more favourable nearground or subterranean environment. 4. The stock of dead organic matter is an important source of humus for the plant in such sterile and unstable soil. 5. The accumulated litter improves the structure of the soil (Odum 1960, Jensen 1974, Grime 1979, West 1985) and creates diverse microsites by acting as a trap for seeds and other reproductive disseminules across a slope (Griggs 1956, Mehra and Singh 1985).

As in all cases of plant distribution, an intricate combination of edaphic, climatic and biotic factors is responsible for the distribution of alpine cushion plants.

It is possible that the establishment and distribution of cushion plants is facilitated to a considerable extent by the general instability of the site. Jarvis (1974) suggested that soil instability may create many small areas suitable for colonization. Ramaley (1927) concluded that the altitudinal distribution of species depends largely upon structural differences which adapt the species to the several climatic belts of the mountains (Quoted by Holch et al. 1941). The cushion life form with all its advantages, as listed above, may well be understood as such structural adaptation. The main roots of cushion plants lie in the more or less stationary layers of the substratum. Secondary roots are able to invade the unstable parts. Some species, such as *Eriogonum androsaceum* are able to "hold their position" despite extensive soil movement downhill. They produce new individuals at locations above the parent plant, where some parts of the main root are exposed.

The disorderly mixed root branches of *Saxifraga bronchialis* spread in all directions. With age, the prostrate branches become rooted, producing a colony of separate plants originating from one individual.

In other cases plants extending over a large area of soil surface may have a common underground system. For example, *Dryas octopetala* depends for its local distribution mainly on the development of a rhizome system which spreads the plant radially for considerable distances.

E. Summary and Conclusions

From the present study the following conclusions are drawn:

1. While cushion plants have the same aboveground form, their rooting patterns have differing characteristics that are site-dependent.
2. On the SW side, plants show site-dependent rooting patterns, that is, plastic responses to site variation. Due to lack of topographic changes on the NE side, there is a uniform rooting pattern.
3. On ridges and steep slopes, the root systems are one-sided, oriented upslope and parallel to the soil surface. The physical effect of downward movement of loose rock and gravel causes this pattern. The main roots anchor the cushion firmly in nonmoving bedrock.
4. The roots spread wider than the corresponding shoots in all studied species. This is considered a successful reaction to gravel-slides and dry slopes. The high ratio of root-to-top spread can be disadvantageous in terms of competition as plants mostly grow side by side.
5. In the majority of the species studied, the standing crop root/shoot ratio is less than unity. This is attributed to a low rate of turnover of aboveground biomass.
6. Since alpine soils are in general rather nutrient-poor and immature in development, litter accumulation by cushion plants represents a major part of the standing

crop and is viewed as an adaptive strategy.

7. The packing material of cushion plants encourages the process of adventitious rooting, protects the growing points, and represents a source of humus to the plant.
8. The widely distributed species in the area have well developed root systems. This can be facilitated by: a) soil instability, which creates many small areas suitable for colonization; b) plastic response of roots to site variation which adapt the species to different edaphic conditions; and c) the ability of the roots to invade the unstable parts of the substratum.

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V. Seed Germination Characteristics and Young Seedling Growth

A. Introduction

The study of seed germination and seedling establishment of terrestrial plants has been the subject of much research. Recent reviews by Koller et al. (1962), Stebbins (1972), Thompson (1973), Evenari (1980/1981), Mayer and Poljakoff-Mayber (1982), Fenner (1985), Bewley and Black (1985) have shown the different facets of such studies.

There have been many attempts to characterize the seed germination behaviour of many plant groups in different geographical areas, where each habitat poses its own particular problems for plant survival (Abdel-Rahman and El-Monayeri 1967, Thompson 1970a and b, Oomes and ElBerse 1976, Bostock 1978, Grime et al. 1981, Freedman et al. 1982 and many others). Among the investigated plants, alpine species have not been studied extensively, perhaps because of (1) their relative unavailability and minor economic importance (Sayers and Ward 1966); and (2) the general replacement of sexual by vegetative reproduction in most alpine and arctic plants. Some aspects of the seed germination of alpine plants have been investigated by Nichols (1934), Mirov (1936), Soeyrinki (1938/39), Pelton (1956), Bliss (1958), Mooney and Billings (1961), Amen and Bonde (1964), Bonde (1965a and b), Amen (1966), Sayers and Ward (1966), while others reviewed and discussed similar studies (Billings and Mooney 1968, Savile 1972, Billings 1974, Grime 1979, and Jolls 1982). None of these studies has resulted in a complete description of germination characteristics and seedling establishment. Furthermore, cushion plants as one of the most distinctive lifeforms of alpine and arctic vegetation have received relatively little attention. The available data are too fragmentary for accurate conclusions about cushion plant seed biology.

A knowledge of the range of environmental requirements for seed germination is important to evaluate (1) the extent to which sexual reproduction contributes to the propagation and distribution mechanisms of cushion plants; and (2) the prospects of using seeding as a mechanism for revegetation after human disturbances. According to Larcher (1980), it is not sufficient that the individual plants simply withstand extreme situations and perform their vegetative functions adequately. The requirements for flowering and for the ripening and germination of seeds must be met.

Bonde (1965b) concluded that the study of dormancy, effects of varying temperatures, light, and scarification on seeds of alpine plants is required to determine the nature of germination behaviour in the alpine environment.

Since seeds from the same population or even from the same individual may differ in germination requirements, various treatments are necessary (temperature, light, stratification, washing and drying, growth promoters) in attempts to stimulate germination. Seed responses to such treatments will provide some information to explain the causes of seed dormancy in each species. Similarly, many researchers applied various procedures to seeds subjected to a range of pretreatments (Pelton 1956, Steinbauer and Grigsby 1957, Sayers and Ward 1966, Junttila 1970, Farmer and Hall 1970, Tool 1973, McLeod and Murphy 1977, Vincent and Roberts 1977, Bostock 1978, Roberts and Lockett 1978, Baskin and Baskin 1976 and 1980, Grime et al. 1981, and Jain 1982).

The objectives of the present investigation were (1) to study the effect of different treatments of temperature, light, simulated water stress and excess, stratification, and four growth regulators (thiourea, potassium nitrate, gibberellic acid and kinetin) on seed germination of six alpine cushion plants; and (2) to explore the effects of chilling and dehydration on young seedling establishment.

B. Material and Methods

Seeds of six species were collected at fruiting time (during August 1983) from natural populations on Mt. Allan at an elevation of about 2250 m above sea level). To standardize the collection times and seed maturation, seed samples were collected from individuals of one population in a closely defined phenological stage after West and Wein (1971): fruit maturation, yellowing of leaves stage. The dry fruits were collected from living plants at one locality for every species. They were placed in paper bags and further air dried in the laboratory for one week after collection. The seeds were then separated from debris by passing through a series of screens. In this way most of the debris and unfilled or shrunken seeds were excluded. The ripe, undamaged seeds were further hand-sorted, and unfilled seeds were removed. The sorted seeds were placed in tightly closed glass vials to slow the rate of food storage depletion, and stored in the dark at room temperature (approximately 20°C). The germination experimental work was conducted on all species studied one month after seed collection, and was completed through a six-month period.

All germination tests were done in covered glass petri dishes (9 x 1.5 cm) on two layers of filter paper (Whatman no.1). Seeds were first placed in every dish, and then the filter paper was moistened to its full water holding capacity (3 ml distilled water or test solution). The tests were performed with 100 seeds each. The dishes were transferred to controlled growth chambers and germination counts were made every day for 10 days. Space limitation and time dictated the termination of every experiment after 10 days. Distilled water was added when necessary to keep the filter paper moist, and excess water was drained off carefully. Seeds were considered to have germinated when the radicle had emerged from the seed coat. At the end of every test, the mean length of roots and shoots of seedlings was measured.

The seeds which remained ungerminated after treatment were tested for viability by 1% triphenyl tetrazolium chloride (TTC). The embryos were squeezed out from the seed coat and placed in a vial containing TTC for about 3 to 6 hours in the dark, and then examined under a dissecting microscope. Viable embryos developed a red colour. Three species showed more than 90% seed viability (*Potentilla uniflora*, *Saxifraga bronchialis* and *Silene acaulis*) and three species showed about 75-80% viability (*Eriogonum androsaceum*, *Saxifraga caespitosa* and *Dryas octopetala*). Viability of the seed stocks did not change significantly during the six-month experimental period.

Germination was then expressed as a cumulative percentage of viable seeds present (germinating plus viable, ungerminated seeds).

The germination value (GV) was used for making objective comparisons among different species and treatments through the test period. The most valuable feature of the germination value is the expression of speed and totality of germination, and their interaction, as a single numerical value (Czabator 1962).

$$GV = PV \times MDG$$

where PV is the peak value, and MDG is the mean daily germination. The range of GV is from zero to infinity. The methods of analysis are described by Czabator (1962).

Temperature

The influence of constant day/night temperature on germination was determined at 5°C ± 1°C increments between 10°C and 35°C. During thermoperiod trials (20/10, 25/15 and 30/20°C) the growth chambers were programmed for 14 hours at the high temperature with light (day) and 10 hours at the low temperature in darkness. This fluctuation in temperature was expected to stimulate the germination of certain species.

Light

The temperature experiments were conducted under three light treatments (light, dark, and alternating light/dark). Lighting was by white fluorescent tubes supplemented by about 20% incandescent light. This gave an approximation for low daylight, except in being deficient in far red light (Bostock 1978). The intensity of light at the surface of petri dishes was about 600 $\mu mol.m^{-2}.sec^{-1}$ (fluorescent and incandescent sources). The dark treatment plates were wrapped with aluminum foil to exclude light. The plates were unwrapped every day to permit gaseous exchange and to make observations. The dark period was broken for approximately 3 minutes during the daily counts which were made under dim light. Under alternating light/dark treatment, the day length was 14 hours, and the plates were wrapped with aluminum foil for 10 hours. The three light treatment plates were placed in the same growth chamber under continuous light.

Stratification

Stratification was accomplished by storing the moist seeds in cheese cloth bags at +2°C in the dark after imbibition at 20°C for 6 hours. Stratification periods were 10, 20, 30, 40 and 90 days prior to the standard germination test. Germination of stratified seeds was done under constant 24°C, 14 hour day length. This treatment may be a factor acting to reduce dormancy of the seeds.

Seed Washing and Drying

In the field, seeds are exposed to wetting (washing) after showers and at times of snow melt. In the summer, they often dry up due to strong winds. This washing and drying may stimulate seed germination by removal of germination inhibitors from the seed coat. This was simulated by washing the seeds in running tap water for 24 hours. Then, the seeds were dried at laboratory temperature (20°C) for one week, after which germination was conducted at constant 24°C, 14 hour day length. In this experiment five replicates were used with 50 seeds each. In the timing of the lab work this experiment was the last; enough seeds were remaining.

Water Availability

Germination was tested under both osmotic drought and substrate water content. Drought was simulated by osmotic solutions of two commonly used substances: Mannitol and sodium chloride with concentrations adjusted to give osmotic potentials of 1, 3, 5, 7 and 10 (-bars). Aqueous mannitol solutions were prepared according to the formula given by Helmerick and Pfeifer (1954): Osmotic pressure (P) = gRT/mv; grams mannitol (g) = Pvm/RT; where v is the volume in liters, m is the molecular weight of mannitol, R = 0.08205 liter atm. per degree per mole, and T is the absolute temperature. Solutions of sodium chloride were derived from a calibration curve of solute potential vs. concentration. Distilled water was used to produce an osmotic potential of zero.

The effect of varying substrate water content (a method modified from Bostock 1978) on germination was examined using six treatments with different volumes of distilled water per dry weight of filter paper substrate. The wettest treatment had a film (2mm) of free water, while the driest was barely moist. Plates were wrapped in polyethylene bags to minimize evaporation. Loss of water by evaporation was found to be negligible. These tests were conducted at constant 20°C, 14 hour day lengths.

Growth Regulators

Four dormancy-breaking substances (gibberellic acid, kinetin, thiourea and potassium nitrate) were used as germination media. Each of them was dissolved in distilled water and diluted to different concentrations (from 5 to 1

-log molar). The seed germination was tested at constant 24°C, 14 hours day length with different concentrations of the four substances. Distilled water was used for the control treatment.

Chilling and Drought Tolerance

Successful seed germination does not ensure seedling establishment in an alpine environment. Due to strong wind and low temperatures, germinating seeds and seedlings may be subject to dehydration and chilling. To ascertain whether the young seedlings remain viable after dehydration or chilling, a modified procedure after Friedman et al. (1981) was used.

The seeds were germinated at constant 24°C, 14 hour day length. The young seedlings (the radicle and plumule had emerged from the seed coat) were removed from the plates and placed on a double layer of dry filter paper. For dehydration treatment, 350 ten day-old seedlings per species were left to dry on the bench at laboratory conditions (20°C, 65% RH) while 350 other seedlings were transferred into a controlled germination chamber for chilling treatment (+2°C, 14 hr day length). Samples of 50 seedlings per species were removed from the treatments at intervals of 3, 6, 9, 12, 18, 24 and 48 hours. Subsequently, they were rewetted and restored to the previous germination conditions. The further development of the seedlings after the treatment was evaluated 3 days after rewetting.

The rewetted seedlings were considered viable when their rootlets continued growing, the cotyledons spread apart or a third leaf expanded, and when they were turgid in appearance. Dead seedlings were slimy and infected with fungi.

C. Results

In one of the six species studied (*Saxifraga caespitosa*), germination did not occur under any treatment. Among the other five species, there were considerable differences in response to germination treatments. The experiments were terminated after 10 days. There may have been more germination if the experiments had continued longer, but as the data for cumulative germination show, germination curve levelled off in most of the treatments.

Response to Temperature and Light

The effects of temperature, light and their interactions on the germination of seeds are not independent of each other. Germinability under different light treatments can be drastically modified by temperature (Appendix 6).

For constant temperatures, several features were apparent. Most striking was the failure of three species to germinate at low temperatures (10°C or colder). Only two species, *Potentilla* and *Dryas* showed some germinability at 10°C (Fig 5.1). Optimum germination temperatures were close to 25°C except for *Dryas* (30°C). Minimum temperatures were very close to 15°C while maxima were over 30°C. At temperatures higher and lower than the optimum, initial and final germination were delayed. *Potentilla* and *Dryas* were able to germinate over a wide temperature range, from less than 10°C to more than 35°C, while *Saxifraga bronchialis* tended to germinate over a narrow temperature range (15 to 30°C). In both *Eriogonum* and *Silene*, germination was restricted to an intermediate temperature range from 10 to 30°C and 15 to 35°C, respectively.

Germination at alternating temperatures was better than the average germination at constant temperatures, but there were considerable differences among species in response to treatments. (Fig. 5.1) The highest average cumulative germination percentage for *Potentilla* seeds was 80% and was obtained with alternating temperatures of 20°C day/10°C night. In contrast, for *Silene* and *Dryas*, germination was highest with a 30/20°C temperature regime and lowest at 20/10°C. *Eriogonum* and *S. bronchialis* showed similar responses to alternating temperatures. Highest germination was obtained under the 25/15°C temperature regime.

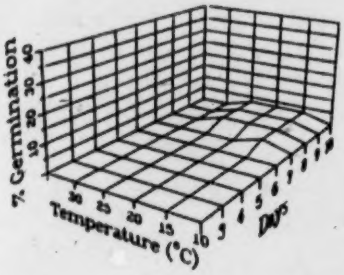
Inter- and intraspecific differences occurred among species in response to the light treatments. At one extreme was *S. bronchialis*, with positively photoblastic seeds, that is, germination was stimulated by light.

0

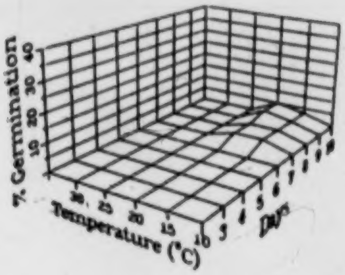
Figure (5.1): Effect of temperature and light and their interaction on seed germination of the different species.

Eriogonum androsaceum

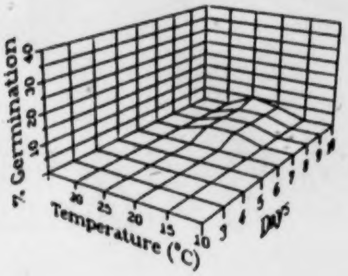
LIGHT



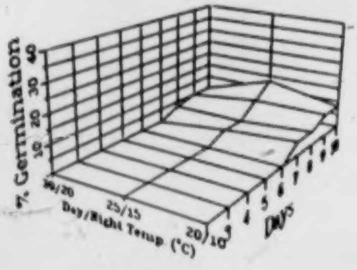
DARK



LIGHT/DARK - CONST. TEMP.

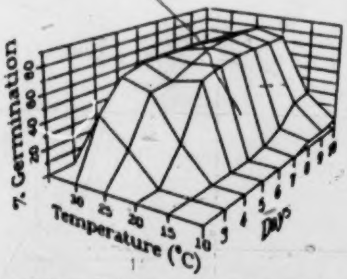


LIGHT/DARK - ALT. TEMP.



Potentilla uniflora

LIGHT



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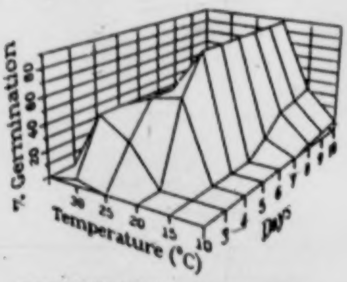

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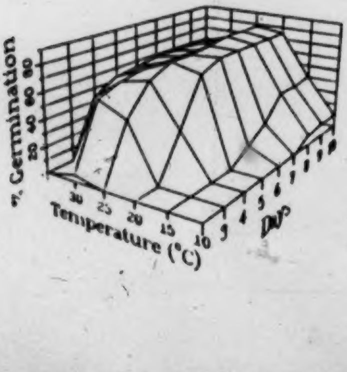
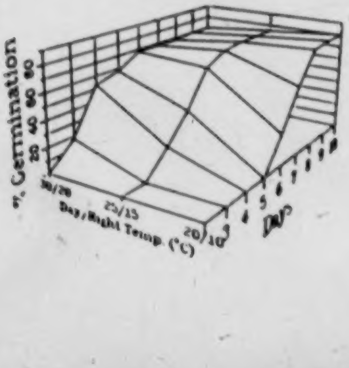
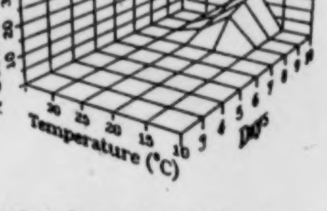


LIGHT/DARK - ALT. TEMP.



Saxifraga bronchialis

LIGHT



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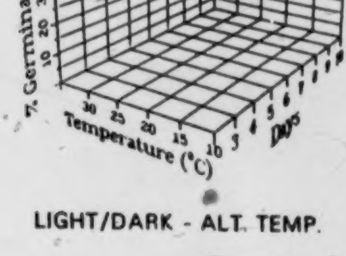
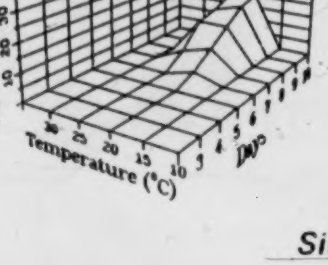
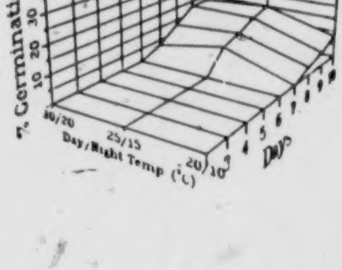


LIGHT/DARK - CONST. TEMP.

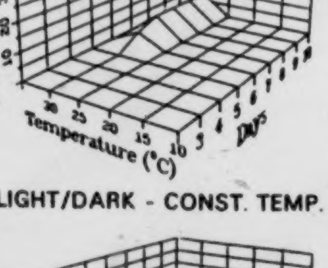


LIGHT/DARK - ALT. TEMP.



Silene acaulis

LIGHT



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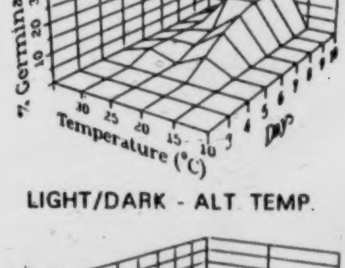
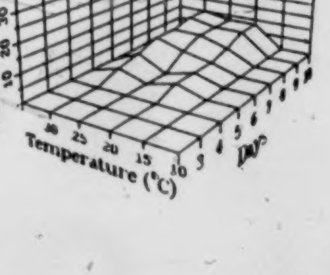
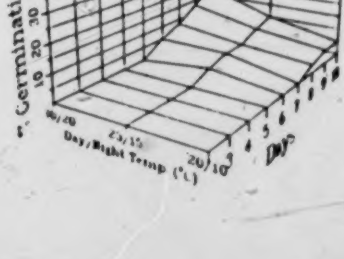


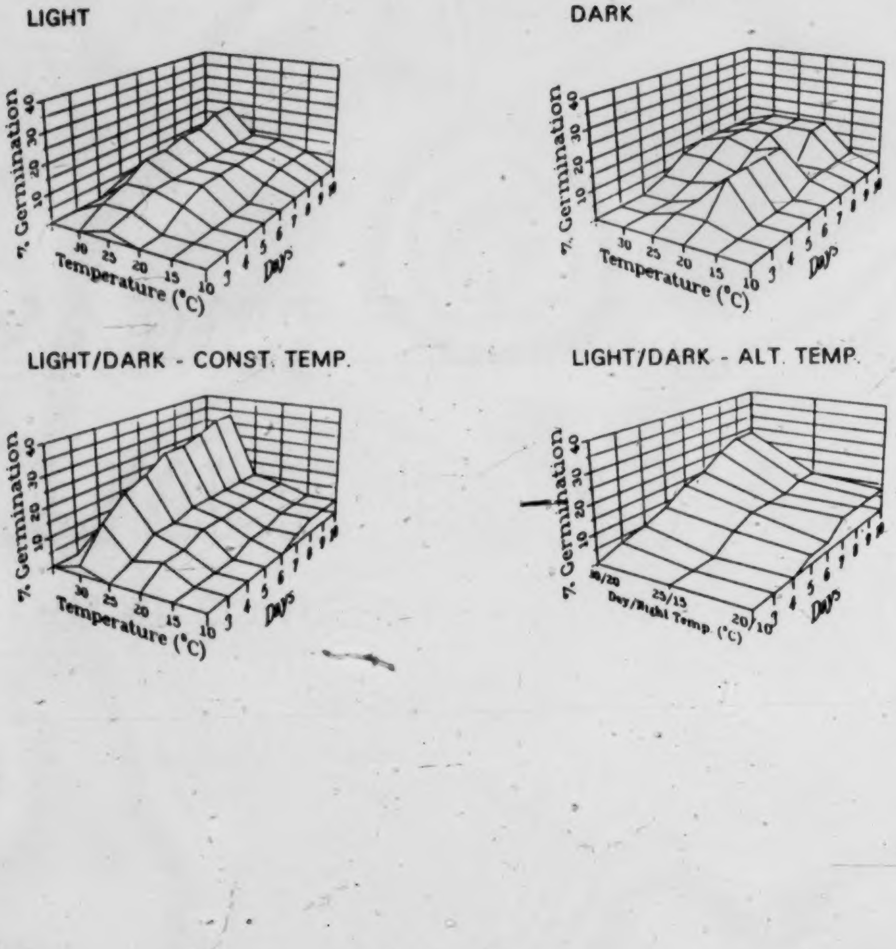
LIGHT/DARK - CONST. TEMP.



LIGHT/DARK - ALT. TEMP.



Dryas octopetala



LIGHT

DARK

LIGHT/DARK - CONST. TEMP.

LIGHT/DARK - ALT. TEMP.

At the other side was *Silene* with negatively photoblastic seeds, that is, light inhibited germination. Germination of the seeds of the other three species was not affected by light, that is, their seeds are non-photoblastic.

The negatively photoblastic seeds of *Silene* were significantly inhibited by continuous illumination and germinated in darkness at temperatures of 25°C and below. Germination falls off at higher temperatures and the seeds became light requiring. This behaviour cannot be explained at present in a simple and convincing way (Smith 1975). At 35°C, germination is prevented completely both in dark and light, and the seeds become thermodormant, that is, photoblastism is affected by temperature. In a manner analogous to the behaviour of *Silene*, germination of *S. bronchialis* is prevented by high temperatures (30°C) irrespective of light conditions. It is noteworthy that the highest germination percentage in the dark of the non-photoblastic species at constant temperature was about 20°C.

Potentilla has a high total germination percentage (close to 80%) around the optimum temperature in all light treatments. In contrast, the other species' germination remained relatively low (below 20%), indicating low responsiveness to both temperature and light.

Germination is markedly promoted by alternating light/dark treatment in *Dryas* and *S. bronchialis*. In contrast, this treatment was not effective in the other three species.

The germination value (GV) provides objective comparisons of germination among species. The germination at constant temperatures in *Eriogonum* was associated with consistently very low GV, ranging from 0.11 to 0.28. Alternating day/night temperatures brought about a considerable increase in GV up to 1.69 (App.6.A). *Potentilla* attained the highest GV among all species studied. It ranged from 0.64 at 10°C to 154.88 at 20°C. Alternating temperatures did not bring about a considerable increase in GV (App.6.B). The other three species exhibited low GV, but their GV's were a little higher than those of *Eriogonum* (App.6.C.D.E.). In alternating light/dark conditions, the GV's are higher than in continuous light.

Response to Stratification

The experiment was terminated after 10 days. In the two species *Silene acaulis* and *Saxifraga bronchialis* seeds were still germinating when the experiment ended. *Potentilla uniflora* and *Dryas octopetala* had almost reached their maximum germination (Fig.5.2). In *Eriogonum androsaceum*, germination was totally inhibited after 20 days of stratification. Seeds of *D. octopetala* showed no stimulation by stratification.

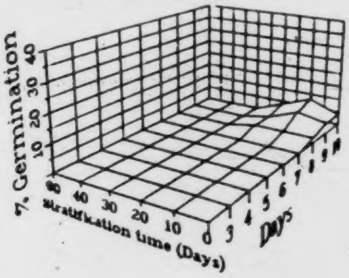
Among the species which responded positively to stratification, there were marked differences not only in germination percentage, but also with respect to GV (GV for

S. bronchialis higher than for *P. uniflora*, GV for *P. uniflora* higher than for *S. acaulis*, GV for *S. acaulis* higher than GV for *E. androsaceum*). At one extreme was the positively photoblastic *S. bronchialis*, where the germination percentage after 10 days of stratification increased 64 percentage points (from 18% to 82%) and the GV increased from 3.24 to 67.24 (App.7). At the other extreme was *E. androsaceum* with rare germination (maximum 4%), but germination was doubled to 8% after 10 days of stratification. No germination occurred after 20 days of stratification. The germinability of *P. uniflora* increased from 60% to 94% and remained high. Even after 90 days of stratification it did not fall below 72%. The GV increased from 51.43 to 220.9. For *S. acaulis*, the maximum germination percentage attained was reached after 20 days of stratification (26%), increasing by 13 percentage points (from 13% to 26%). There was no pronounced increase or decrease in GV with increase in the stratification period. In most species, stratification to certain periods promoted seedling growth (App.7).

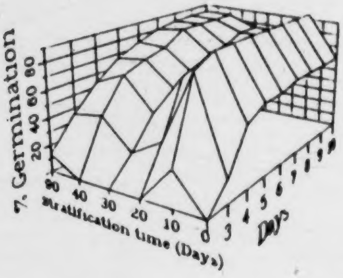
Qualitatively, seeds of all species responded to stratification periods in the same way. This holds true despite quantitative differences among species.

Figure (5.2): Effect of stratification time on seed germination of the different species at constant temperature of 24°C and 14h day length.

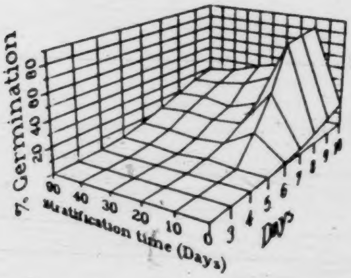
Eriogonum androsaceum



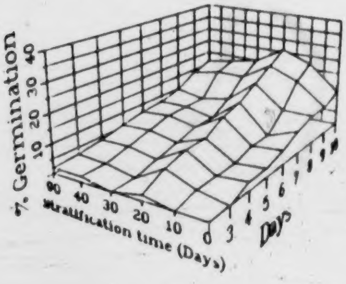
Potentilla uniflora



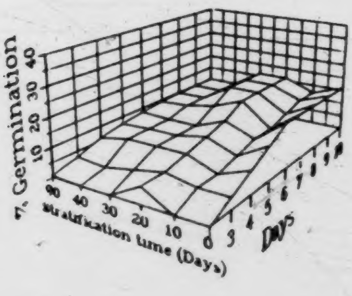
Saxifraga bronchialis



Silene acaulis



Dryas octopetala



Response to Washing and Drying

Washing and drying experiments were performed because the percentage of germination in seeds was not as high as expected, and it was thought that leaching might improve germination. When intact seeds were leached with running water to remove some inhibitors, germination was increased. When seeds were washed and dried prior to germination, the t-Test indicated a significant increase in total germination and GV of all species except for *P. uniflora* after 10 days. In contrast, the differences between seedling root and shoot lengths were not significant in four species. Only in *P. uniflora* was there a significant increase in root growth at the 95% probability level, with root growth increasing from 26.8 mm in dry stored seeds to 30.2 mm for washed/dried seeds (App.8). Dry stored seeds of *S. acaulis* gave only 12% germination at 24°C, but the washing/drying treatment induced better total germination of 36% after 10 days (Fig.5.3). In the remaining three species, *E. androsaceum*, *S. bronchialis* and *D. octopetala*, germination of leached seeds was almost twice that of dry-stored seeds.

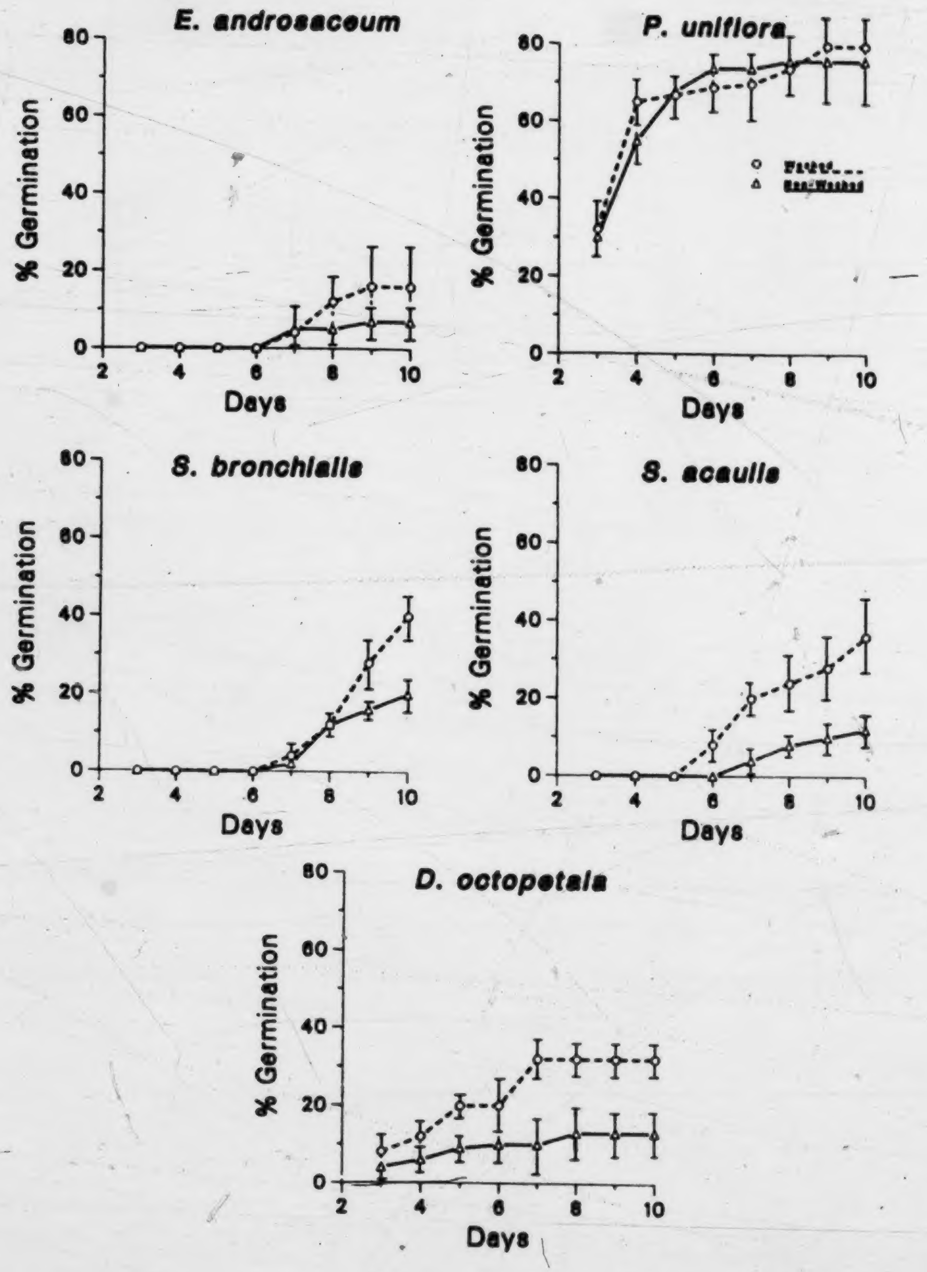


Figure (5.3): Effect of washing and drying of seeds on seed germination of the different species at constant temperature of 24°C and 14h day length
(o-----o washed; Δ——Δ non-washed).

Response to Water Availability

Germination of the seeds and the growth of seedlings of *P. uniflora* and *S. acaulis* decreased with decreasing water potential. This was generally true for both mannitol and sodium chloride osmotic solutions, but the rate of response differed (Fig.5.4). The germination of *S. acaulis* seeds ceased at water potentials equal to or exceeding -5 bars with mannitol, and ceased at -10 bars or more with sodium chloride. For *P. uniflora* the data did not show a point where germination and growth of seedlings ceased, but the higher the osmotic concentration of the solution, the lower were the germination percentage and seedling growth.

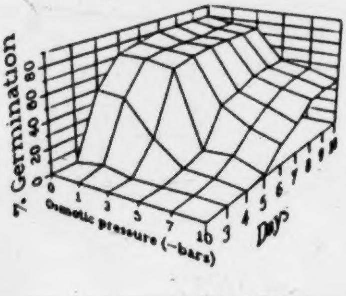
On an iso-potential basis, that is, equal osmotic concentrations of the two solutions, the reduction in germination was greater for *S. acaulis* seeds with mannitol than with sodium chloride. For *P. uniflora* the reduction was higher at concentrations of -5 bars or more with mannitol than with sodium chloride. The time when the germination curve levelled off, that is, when no additional sizeable germination occurred, was influenced by the level of osmotic potential. To a great extent, the levelling-off time was similar for mannitol and sodium chloride in the two species. The reduced water potential of the two osmotic solutions suppressed root growth more than shoot growth in the two species (App.9.A).

0

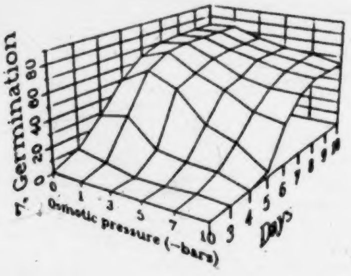
Figure (5.4): Effect of water stress (Osmotic pressure) and substrate water content on seed germination of *Potentilla uniflora* and *Silene acaulis* at constant temperature of 24°C and 14h day length.

Potentilla uniflora

Mannitol

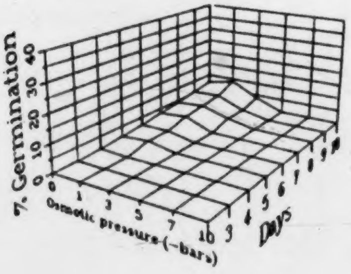


Sodium chloride

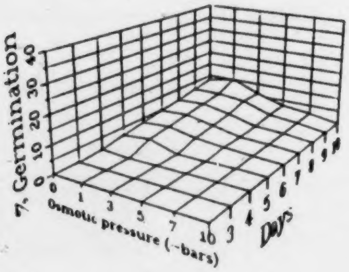


Silene acaulis

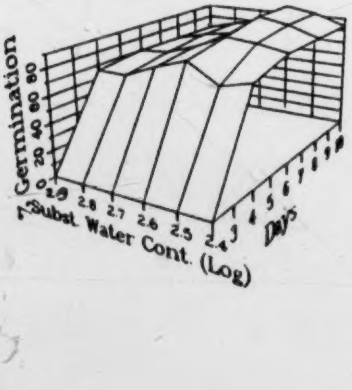
Mannitol



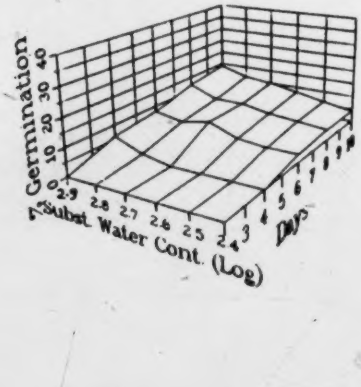
Sodium chloride



Potentilla uniflora



Silene acaulis



S. acaulis showed a linear response to changes in the water content of the substrate, that is, germination increased with SWC. (Fig.5.4; App.9 B). Drier substrates reduced the efficiency of seed-substrate contact, so that the rate of germination decreased. *Potentilla uniflora* showed an optimal SWC for seed germination.

Response to Growth Regulators

The application of various concentrations of two non-hormonal substances (thiourea and potassium nitrate) and two hormonal substances (gibberellic acid and kinetin) was tested to determine the optimal concentration for eliciting seed germination and seedling growth. These four substances are known to have a stimulating effect on seed germination and seedling growth.

Various concentrations of thiourea as a germination medium caused an apparent inhibition in seed germination and seedling growth of *E. androsaceum* and *S. acaulis*, while its effect on germination of *P. uniflora* and *S. bronchialis* seeds was a function of thiourea concentrations (Fig.5.5). The best germination attained by *P. uniflora* was at 2(-log mol). *S. bronchialis* seeds showed best germination at the low concentration of 3.3(-log mol). Shoot growth of *P. uniflora* was promoted at the very low concentration of 3.3(-log mol), and root elongation was inhibited regardless of the thiourea concentration (App.10.B). Despite the inhibitory effect of thiourea on seed germination of *D.*

octopetala, the seedlings grew taller than non-treated control seedlings (App.10.E). This was in contrast to *S. bronchialis* (App.10.C). It is clear that thiourea has different effects on seed germination and seedling growth of cushion plants.

Seed treatment with potassium nitrate as a germination medium improved germination in four of the five responding species (Fig.5.5). The seeds of *E. androsaceum*, *S. bronchialis* and *D. octopetala* showed a general increase in germination in most of the concentrations tested, showing an optimum of 3.3(-log mol), 2(-log mol) and 1.7(-log mol), respectively. Germination of *P. uniflora* was markedly stimulated at all concentrations used. For *Silene acaulis*, germination was inhibited by potassium nitrate regardless of the concentration. Root and shoot growth of the seedlings were inhibited or attained no elongation in all species tested, with the exception of *E. androsaceum* (App.10.A), where seedling growth was promoted at a potassium nitrate concentration as low as 3.3(-log mol).

Gibberellic acid (GA_3) produced different effects on seed germination and seedling growth of the five species.

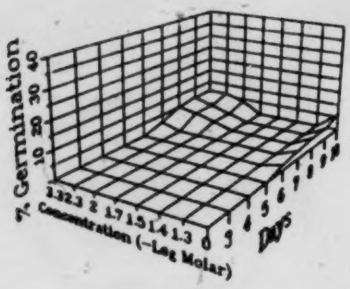
The germination of four species was promoted, but there was no promoting effect in *D. octopetala* (Fig.5.5).

0

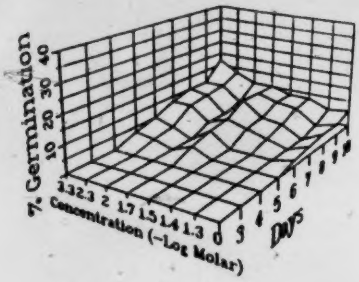
Figure (5.5): Effect of four growth regulators on seed germination of the different species at 24°C and 14h day length.

Eriogonum androsaceum

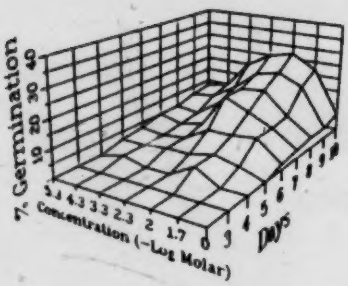
Thiourea



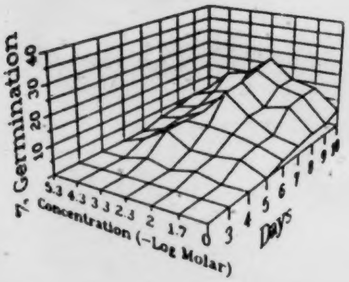
Potassium nitrate



GA$_3$

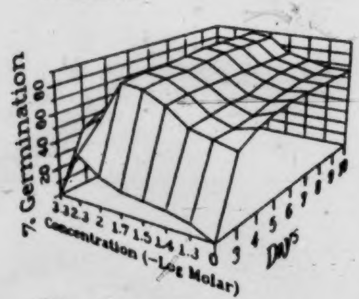


Kinetin

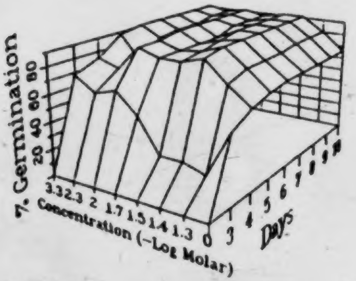


Potentilla uniflora

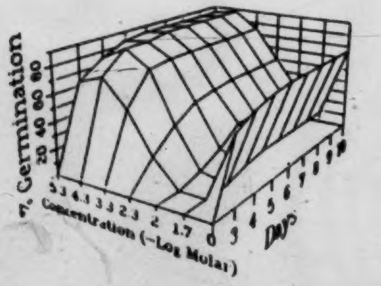
Thiourea



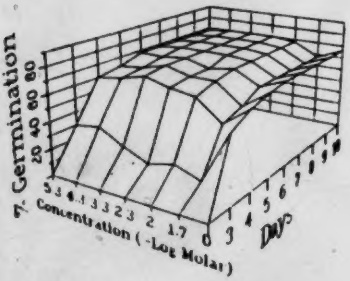
Potassium nitrate



GA$_3$

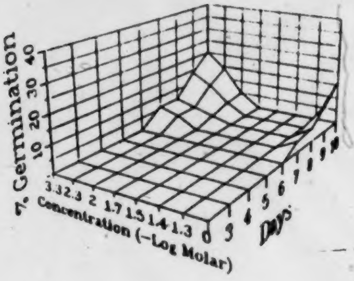


Kinetin

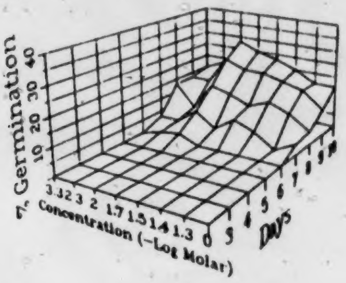


Saxifraga bronchialis

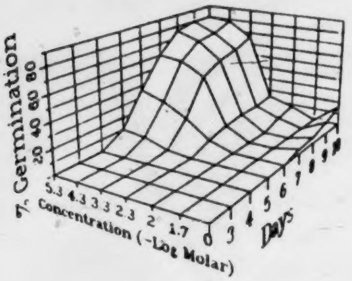
Thiourea



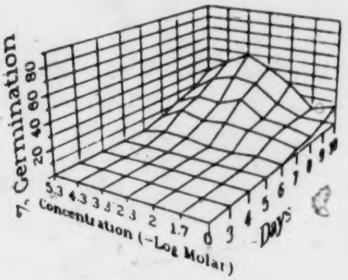
Potassium nitrate



GA_3

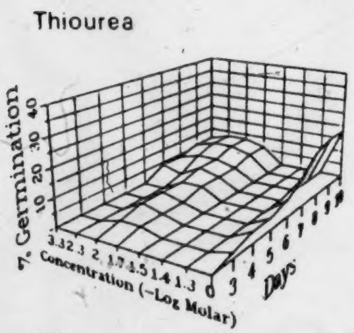


Kinetin

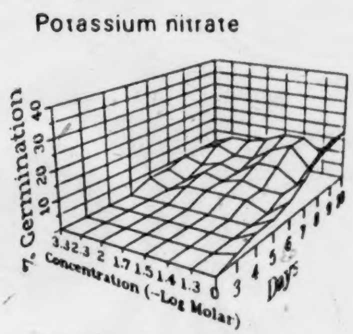


Silene acaulis

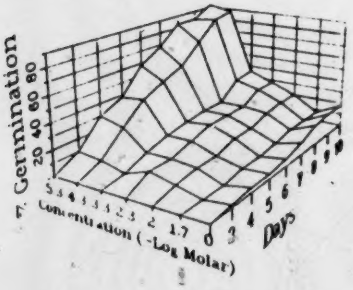
Thiourea



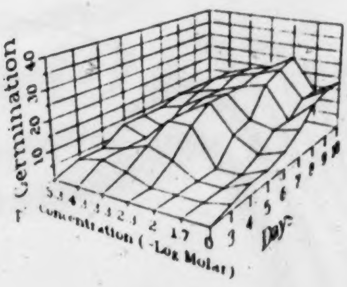
Potassium nitrate



GA_3



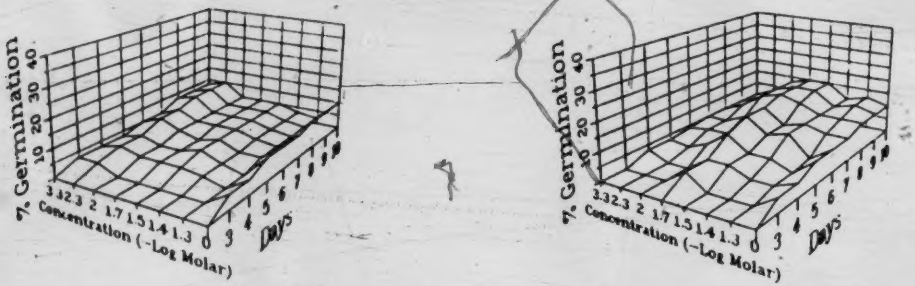
Kinetin



Dryas octopetala

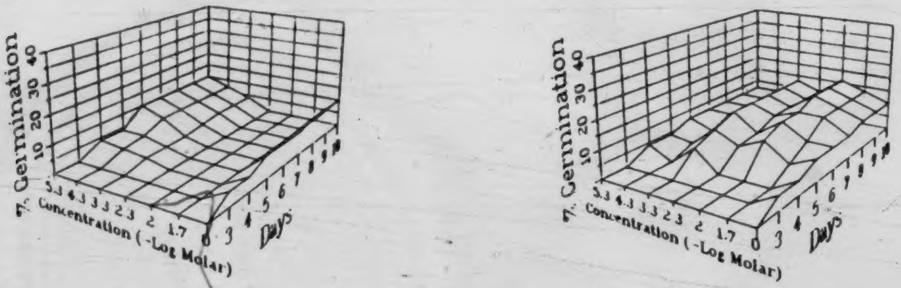
Thiourea

Potassium nitrate



GA$_3$

Kinetin



A gradient response was obtained using various concentrations of GA_3. Seeds of *E. androsaceum* had the best (optimum) germination response at a concentration as high as 2(-log mol), while *P. uniflora*, *S. bronchialis* and *S. acaulis* showed optimum responses at low concentrations, 4.3(-log mol) and 5.3(-log mol). There was a marked reduction in seedling root growth of all species, except for *S. acaulis* (App.10.D). This was probably due to a toxic effect on root growth caused by prolonged soaking in GA_3 during the germination period. In contrast, the shoots grew taller than the non-treated control seedlings, except for *Eriogonum androsaceum*, where shoot growth was reduced about two times due to GA_3 treatment (App.10.A).

Kinetin increased germination of seeds in all five species. Four species showed an optimal response to varying concentrations of kinetin as a germination medium (Fig.5.5). The optimum concentration for *E. androsaceum* seeds was 2.3(-log mol), while for *Potentilla uniflora* and *S. bronchialis* it was 3.3(-log mol). *S. acaulis* seeds had optimum responses at the high concentration of 2(-log mol). *Dryas octopetala* germinated better at higher concentrations of kinetin. However, the GV of *D. octopetala* seeds (App.10.E) fluctuated with different concentrations, making it difficult to relate germination directly to a given concentration. Root and shoot growth were influenced by kinetin treatment. Reductions in root elongation were apparent in all species, except in *S. acaulis*, where a remarkable extension occurred regardless of the concentration used (App.10.D). In contrast, shoot growth was increased in response to kinetin in all species, with the exception of *E. androsaceum* seedlings (App.10.A).

Generally, the stimulation of seed germination and seedling growth by different growth regulators is a function of its concentrations showing an optimum.

Seedling Response to Chilling and Dehydration

The duration of both chilling and dehydration affected seedling survival markedly. Dehydration had a stronger impact than chilling. The duration of exposure played an important role. Survival was much better under short treatments (Fig.5.6; Appendix 11). No seedlings survived dehydration for a full 48 hours, with the exception of *P. uniflora*, which showed an 8% survival. Generally, in the three species investigated there was a sharp decline in seedling survival with both treatments. The three species can be ranked according to their relative tolerance to chilling and dehydration as follows: *P. uniflora* > *S. acaulis* > *S. bronchialis*.

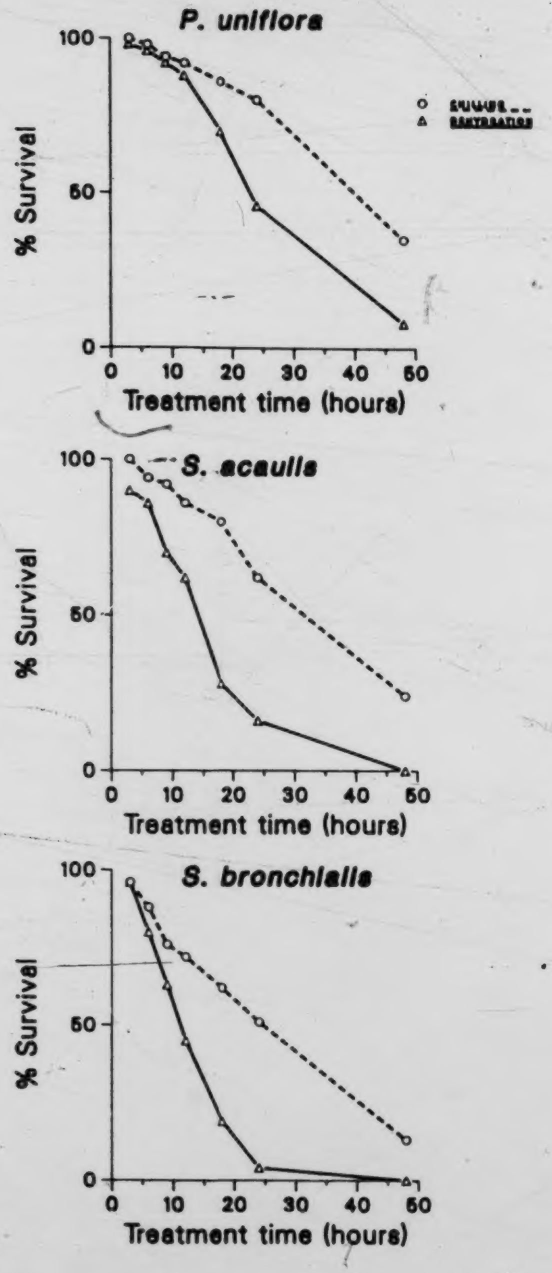


Figure (5.6): Effect of chilling and dehydration on seedling survival and establishment of *Potentilla uniflora*, *Silene acaulis* and *Saxifraga bronchialis* (o-----o chilling; Δ——Δ dehydration).

D. Discussion

Temperature and Light

One can analyze the relative suitability of alpine habitats for the germination of cushion plant seeds by comparing the results of the present study with germination trials in other areas. In the present study, 13% and 18% of *D. octopetala* seeds germinated around the optimum temperature in the dark and light, respectively. These percentages doubled under alternating day/night. Soeyrinki (1938-39) tested seeds of this species from Finland and reported 40% germination in the dark, while Bonde (1965b) found 10% germination in alpine Colorado. Elkington (1971) found 48% germination in light on seeds from Britain, and Soerensen (1941) reported germination of seeds from Greenland, but did not give quantitative data.

Only 23% of the seeds of *S. acaulis* germinated after 10 days in the dark at 25°C, while germination was totally inhibited by light. Bliss (1958) found that *S. acaulis* seeds from Wyoming kept in the dark germinated slightly better than seeds in light. Bonde (1965a) observed that seed germination improved with time, a maximum 100% being attained after 32 month storage. Also, Bonde (1965b) found 12.5% to 24% germination in *S. acaulis* after 10 days in the dark with seeds from alpine Colorado. These percentages increased after 28 days. Soeyrinki (1938-39) found 95% germination after one week for seeds from northern Finland.

Jones and Richards (1962) reported that *S. acaulis* seeds from northern Wales germinated poorly and light had no effect.

The germination of *S. bronchialis* in this study was nil in the dark. Bonde (1965b) demonstrated that seed germination was very poor in the dark (3%), and began in the third week. The present study's results agree with these findings at least during the experimental period.

The seeds of *S. caespitosa* did not germinate under any tested treatment, but other authors have found germination in seeds from other areas. Soerensen (1941) and Webb (1950) recorded germination in seeds from Greenland and Britain, respectively. Bell and Bliss (1980) found that 65% of seeds from the Canadian high arctic germinated after 28 days at constant 20°C in light. Sixty-four percent germinated after 32 days when seeds were immersed in non-aerated water. There was no germination of *S. caespitosa* seeds immersed in aerated water. Seed germination in the field on test plots in various microhabitats was nil or very low.

The present data and the findings of others show that for different species of cushion plants, there is no uniform germination behavior with respect to temperature and light in different environments. It is beyond the scope of this study to distinguish between modifications within the genetic plasticity and genotypic adaptations, although many authors link germination responses to temperature and light in the latter sense to particular ecological situations

(Koller et al. 1962, Thompson 1970c, Toole 1973, Smith 1975, Harper 1977, Grime 1979, Grime et al. 1981, Mayer and Poljakoff-Mayber 1982, Bewley and Black 1985).

The high temperature optimum for the germination of mountain cushion plant seeds is not surprising. High soil surface temperatures after snow melt on sunny and windless days are well-documented for such areas (Turner 1958, Geiger 1975, Moser 1970, Addy 1986). The bulk of the seeds from the previous year will germinate when the soil is still moist from meltwater and spring rain, but temperatures stay relatively high also during the night. However, favourable conditions usually do not last for long on such sites, since high temperatures and wind soon reduce the soil moisture. It is, therefore, essential for the survival of the seedling to develop roots as deep and as quickly as possible. Sufficient rooting often fails, and seedling establishment is therefore very limited.

Differences in photoblastism (*S. bronchialis* positive; *S. acaulis* negative) do not lend themselves to easy interpretation. One may expect that this mechanism prevents *S. acaulis* from germination on too exposed sites, favouring the establishment of new plants in dark crevices or even within *S. acaulis* cushions. The multiple bulges of *S. acaulis* cushions support this idea. In contrast, the loose *S. bronchialis* cushions, often sitting on crevices of rock outcrops, can obviously grow on very exposed sites. Soil movement downhill may often bury seeds or expose them to full light, and neutral photoblastism of the remaining species would seem appropriate under these conditions.

Stratification

Moisture/low temperature treatment is a common method for breaking dormancy in seeds of several species. The present results indicate that four out of five species investigated have a stratification requirement. In the species which respond positively to stratification, maximum germination increased by between 4 and 64% after 10 days. The reduction of germination with an increase in stratification period (more than two weeks) suggests that seeds are in a slightly deeper state of dormancy after a short period of stratification. This confirms that the timing of the germination is not only controlled by varying environments, but also by changes in the relative dormancy of the seed that occur as after-ripening proceeds. Dormancy in *Saxifraga bronchialis*, *P. uniflora* and *S. acaulis* was less pronounced than in *E. androsaceum* and *Dryas octopetala* seeds. It is noteworthy that seeds of the two more dormant species (*Eriogonum androsaceum* and *D. octopetala*) possess hard testae. Barton (1965) and Amen (1966) concluded that seed coat inhibition is frequent on sites of severe soil disturbance. For cushion plants, soil disturbance (instability) is a characteristic feature of the environment. Natural breaking of dormancy during overwintering in a moist, cold substratum may remove some germination obstacles.

Seed Washing and Drying

As reviewed by Evenari (1949), Wareing (1965), Mayer and Poljakoff-Mayber (1982), inhibitory substances have been considered to play a part in the imposition of dormancy in a large number of seeds, although little is known about their mechanism of action. It has been demonstrated by many authors that in some seeds, germination inhibitors are located in the seed coat, and it has been suggested that the embryo is allowed to germinate because of the removal of the inhibitor. Seed coat inhibition is probably the most common cause of alpine seed dormancy (Amen 1966). Most of the cushion plants on Mt. Allan fit into this picture. Evenari (1949) noted that inhibitors may work by hampering water uptake of seeds, while Barton (1965) noted the possibility of the seed coat imposing dormancy by means of its restriction of gas exchange and water uptake. However, further discussion of the action of inhibitors on germination is beyond the scope of this study.

In the laboratory experiment, washing with running tap water led to promotion of germination. The seeds may not germinate unless water soluble inhibitors contained in the seed coat are washed out through repeated rain and dry spells. This means that germination of the seeds produced in one year is protracted over several periods favourable for germination. If the conditions are unfavourable during one year, germination in the following year is assured by the reserve of germinable seeds. In the field, leaching will most likely have an even higher effect on germination than the laboratory experiments show. The inhibitors are washed out from the germinating seeds, whereas this does not happen on the moist filter paper in the petri dishes, where the leachate remains in contact with the seeds.

Water Availability

The study of the effect of soil moisture stress on seed germination and seedling establishment has become a prominent issue in the recent literature.

Two osmotic substances were used (mannitol and sodium chloride) to simulate drought. Although these simulated conditions do not precisely represent natural conditions, they allow a rational interpretation of relevant processes. One important aspect is the inhibitory effect of decreasing water potential (Doneen and MacGillivray 1943, Uhvits 1946, Ayers 1952, Collis-George and Sands 1962, Collis-George and Hector 1966, Koller 1967, Kaufmann and Ross 1970, Sharma 1973, Hegarty and Ross 1978). Others are the effects of the substrate water content (Collis-George and Sands 1959, Sedgley 1963, Harper and Benton 1966, Negbi et al. 1966, Oomes and Elberse 1976, Bostock 1978, Oberbauer and Miller 1982).

The results indicate that at high concentrations (5atm or more) germination decreases. The reduced water potential of the surrounding medium makes imbibition difficult, and germination is inhibited. However, Sharma (1973) reports that osmotic substrates of low molecular weights (sodium chloride and mannitol) may enter germinating seeds and induce effects, including toxicity, that are more complex than true drought.

Regarding the influence of SWC, a study by Harper and Benton (1966) suggests that a seed on the surface of a water supplying substrate will both absorb water from the substrate and lose water to the atmosphere. In order to germinate, the seed must show a net gain of water. The present results show that at higher SWC, the area of seed surface in contact with water is large; and the rate of water uptake exceeds the rate of water loss from the seeds. The seeds are therefore able to germinate. At low SWC, the contact area with water is small, the balance is negative and germination cannot take place. However, excessive SWC can also be harmful, as the results with *P. uniflora* demonstrate. This suggests that because of the coarse soil supporting cushion plants with its reduced capillarity and water holding capacity, the soil water content can be a dominant factor controlling germination on alpine dry slopes.

It is noteworthy that *P. uniflora* seeds, which can germinate over a wide range of conditions of osmotic drought, require an optimal SWC for germination (optimal response) (Fig.5.4, App.9.B). In contrast, *S. acaulis* seeds, which are more specific, (that is, germinate under a narrow range of osmotic drought) require a high substrate water content for better germination (linear response). The restricted seed germination in this experiment is probably not caused by abundant water itself, but by deficient air supply which restricts aerobic metabolism in the seeds. McGinnies (1960) and Sharma (1973) pointed out that species germinating under high moisture stress will not necessarily survive drought during seedling establishment or after they mature. However, Pickett and Bazzaz (1978) have shown that responses of the seeds to the moisture gradient are narrower than the responses of adult plants.

Seeds show the same response pattern to an increase in water supply as they do to an increase in temperatures, despite the fundamental dissimilarity of these two environmental factors. There is an optimal substrate water status for percentage germination and seedling growth. A comparison of species distribution with germination in response to water availability shows that species germinating well under a wide range of moisture stress conditions are distributed over a wider range of the altitudinal transect (e.g. *P. uniflora*). Species that do not germinate well under moisture stress, e.g. *S. acaulis*, are narrower in their distribution.

The wider distribution range of *P. uniflora* can also be related to its rapid germination if conditions are good. *P. uniflora* had the highest germination values. Under optimal conditions, over 50% of the seeds had germinated in 3 to 4 days (about 80% in 7 days). The relatively short time span between meltwater flow and summer drought can therefore be better utilized by this species.

Growth Regulators

Although research results on growth regulators are quite extensive, it is still difficult to obtain a comprehensive view of what is happening during germination (Stowe and Yamaki 1957, Overbeek 1966, Mayer and Poljakoff-Mayber 1982). Marked differences were found among species as summarized in Table (5.1). Thiourea seems to be the least effective substance in inducing germination. GA_3 is the most effective growth promoter in inducing germination and in giving high GV in three species; *S. acaulis*, *S. bronchialis* and *E. androsaceum*.

The exact mechanisms by which the growth regulators enhance seed germination and seedling growth are not clear, although several possibilities have been noted for other species. Gibberellic acid stimulates embryonic axis elongation through increased cell division, that is, it increases the growth capacity of the embryo (Odegbaro and Smith 1969), and it triggers hydrolytic activity to make soluble sugars available to the embryo through enzyme activation (Overbeek 1966). Kinetin plays a role similar to gibberellic acid.

Table (5.1): Seed germination and seedling growth responses of the different species to four growth regulators.

+ = promotion (function of concentration)

- = inhibition (regardless concentration)

0 = no change

Growth regulator	Item	Species				
		ERAN	POUN	SABR	SIAC	DROC
Thiourea	Germination	0	+	+	-	0
	Root elongation	-	-	-	0	+
	Shoot growth	-	+	+	-	+
Potassium nitrate	Germination	+	+	+	-	+
	Root elongation	+	-	-	-	-
	Shoot growth	+	0	0	-	+
Gibrellic acid	Germination	+	+	+	+	0
	Root elongation	-	-	-	+	-
	Shoot growth	-	+	+	+	+
Kinetin	Germination	+	+	+	+	+
	Root elongation	-	-	0	+	-
	Shoot growth	-	+	+	+	0

It may affect water uptake, either by increasing membrane permeability or by increasing the internal concentration of osmotically active solutes (Boothby and Wright 1962, Kaufmann and Ross 1970). Also, it may reduce the strength of the seed coat, where it stimulates cotyledon expansion through cell division resulting in seed coat rupture (Ikuma and Thimann 1963). It may also interact with and antagonize an endogenous inhibitor (Smith et al. 1968). The actions of thiourea and potassium nitrate on germination are obscure, and no clear-cut conclusions can be drawn about the mechanism by which they stimulate germination and seedling growth. However, Mayer and Poljakoff-Mayber (1982) pointed out that thiourea acts by affecting the respiratory mechanism, possibly by rapidly channelling all respiration in the direction of energy-yielding processes.

After-ripened seeds of the species studied have an initial dormancy which declines under growth regulator treatment, allowing seeds to germinate better. These results are consistent to a great extent with previous studies for other species (Wiggans and Martin 1961, Boothby and Wright 1962, Koller at al. 1962, Ikuma and Thimann 1963, Overbeek 1966, Amen 1967, Ashiru 1969, Odegbaro and Smith 1969, Henson 1970, Junttila 1970, Farmer and Hall 1970, Kaufmann and Ross 1970, Vincent and Roberts 1977, Bewley and Black 1985). One growth regulator may have effects on the seeds of particular species, some of which are parallel and some opposite to those of other regulators.

The application of the two hormonal substances GA_3 and kinetin promoted seed germination and seedling growth of the negatively photoblastic *S. acaulis* more than that of positively photoblastic *S. bronchialis*. In contrast, the two non-hormonal substances thiourea and potassium nitrate promoted better seed germination of *S. bronchialis* and inhibited germination and seedling growth of *S. acaulis*. The three non-photoblastic species differed in their responses to both hormonal and non-hormonal growth regulators. At the same time, the effects of both GA_3 and kinetin on the same species were similar to a great extent. The non-hormonal substances exhibited various effects on germination and seedling growth of the different seeds. It is striking that at some concentrations which triggered germination, root or shoot growth of seedlings was inhibited. The inhibitory effect of GA_3 and kinetin on seedling growth of most species was accompanied by shorter and thicker roots and shoots than observed for the control treatment. The potency of such growth regulators as dormancy breaking substances, and the presence of some of them (e.g. gibberellins in germinating seeds) strongly suggest they play an important role in the natural control of dormancy.

After breaking seed dormancy by stratification and growth regulators in the laboratory, subsequent germination and seedling growth appear to be highly variable among species. Some, e.g. *S. bronchialis*, *P. uniflora* and *S. acaulis*, require cold treatment for effective seed germination. They therefore show apparent correlation with factors of the environment where cushion plants usually occur on snow free areas and seeds are subject to severely cold temperatures during winter. In contrast, the lack of a cold requirement for effective seed germination in many other alpine seeds may be attributed to the insulating effects of snow cover or to the short growing season (Amen 1966). The promotion of germination in response to the hormonal growth regulators GA_3 and kinetin suggests that stratification acts, among other things, by shifting the balance between growth inhibitors and growth promoters.

Seedling Response to Chilling and Dehydration

The ultimate germination percentage or the germination value may be of less ecological importance than the amount of seedling growth and establishment (Gulliver and Heydecker 1973, Oomes and Elberse 1976), where the establishment of seedlings is the weakest link in the colonization of new territory by plant species (Stebbins 1972, Freedman et al. 1982).

This study indicates that drought and chilling can hamper seedling growth significantly. Seedling survival after each treatment period was better with chilling than with dehydration treatments. This indicates that although the temperature may fall below the freezing point on some days and in more nights during the growing season, chilling seems not very critical for the survival of the seedlings.

However, the findings of Sayers and Ward (1966) showed that a high frequency of near or below freezing temperatures in the alpine zone during summer months substantially reduces the amount of germination.

Gulliver and Heydecker (1973) wrote that one of the first effects of progressively drier conditions is the reduction of seedling emergence. On Mount Allan with its coarse gravel soil, seedlings have little chance to establish themselves. However, Billings and Mooney (1968) and Jolls (1982) pointed out that reproduction by seedlings appears to be more important in the drier alpine sites than in any other alpine environmental type. Field observations on Mt. Allan showed drought, manifested in severe wilting, even in mature plants on warm summer days. In spite of root competition, here seedlings may stand a better chance of survival on cushion plant substrate than on bare soil, since the packing material of old cushion plants holds a store of moisture. This may confirm the observation of Griggs (1956) and Hedberg (1964) that seedlings of many alpine plants survive better in the cushion plant substrate and become established before they come into direct physical contact or root competition with their host. In contrast, on bare microsites any slight water shortage is more serious for seedlings than it is for well established individuals.

The combination of dry soils, high insolation, and high soil surface temperatures may create critical conditions for the establishment of cushion plant seedlings in alpine zones. Such conditions were observed by Wager 1938, Billings and Bliss (1959), and Brink (1964). While Mark (1965) found that many seedlings died principally during late summer and autumn, and those which had been lifted by frost in winter were most vulnerable to surface desiccation.

E. Conclusions

Of six species tested, five exhibited germinable seeds upon ripening, and appeared to have different degrees of dormancy (Viable seeds which failed to germinate when tested under conditions suitable for growth were assumed to be dormant). Germinability varied considerably with tested factors, as well as among species. This interspecific variability seems to be a response to different alpine microhabitats. Since the investigated species exhibit different distribution patterns on both windward and lee sides, one may conclude that a correlation between seed germinability and habitat does exist. In this case, alpine cushion plants grow in specific microsites rather than sporadic as in ice-free areas where snow never persists for more than a few hours.

For the present study, the following conclusions can be drawn regarding cushion plant seed germinability and seedling establishment: (1) Non-dormant seeds may germinate immediately after ripening and establish some seedlings in the late summer or early fall. Accordingly, there is a high risk of mortality during the following winter. (2) Dormant seeds undergo a winter quiescence before germination in the following year. (3) Seedlings which are more tolerant to drought and chilling are better endowed to reach a wide range of suitable micro-sites for germination and establishment, thus increasing the distribution of the species over a larger range of both slope and aspect. However, seedling drought tolerance is not necessarily an acceptable index of drought tolerance in mature plants. (4) Seeds deposited on the cushion plant packing material are immediately supported by mineral soil, plant fragments, and available moisture. The packing material modifies the infertile rocky soils through nutrient release and water storage, thus forming an adequate substrate for seedling establishment. These microsites are among the most favourable sites for cushion plant seed germination and seedling establishment. (5) On bare soils, higher rate of root extension than shoot elongation is a prerequisit for successful establishment where the surface soil dries rapidly. (6) The failure of seedling establishment can be due to: a) shortness of the growing season and viable seeds may not be produced by many individuals of the population. b) viable seeds may be eaten by animals or may be blown into unsuitable environments. c) too slow growth due to unfavourable conditions. d) exposure of the vulnerable seedlings to late summer drought and fall chilling before they develop resistance. e) soil disturbance and instability. Seedlings may be killed mechanically.

Although vegetative reproduction is very common and is, perhaps, the primary method by which new plants are formed in alpine sites, it can be inferred that seedlings may contribute to cushion plant regeneration. Although seedlings do not appear numerous, they can be found in the field to bridge gaps of completely unsuitable habitats for vegetative growth. The prospects of using artificial seeding as a method for revegetation after human disturbances may be good, if cushion plant seedlings are produced on a large scale. Their ability to grow on unstable soils, their rooting pattern and their relative drought resistance characterize at least some of them as colonizers of disturbed sites.

F. Summary

This laboratory investigation of alpine cushion plant seed germination and seedling growth suggests the following:

1. Seeds of different cushion plant species differ in their ability to germinate and establish seedlings under alpine conditions. These differences are considered to be inherent to the species, aside from the influence of the environment.
2. Temperatures favourable for seed germination occur from early summer to early fall. In response to light, the seeds can be positively-, negatively-, or non-photoblastic.
3. Most of the investigated species have a stratification

requirement.

4. Seed washing and drying promote germination and seedling growth as well. This is attributed to washing out the water soluble inhibitors from the seed coat.
5. Seeds of local widely distributed species germinate over a wider range of osmotic drought than other species.
6. Growth regulators have different effects on seed germination and seedling growth of the species investigated. They exhibit both stimulatory and inhibitory effects.
7. Under alpine conditions cushion plant seedlings can survive. The main reason for death is drought.
8. In contrast to other alpine plants, sexual reproduction of cushion plants can be as successful as vegetative propagation.

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VI. Carbon Dioxide Gas Exchange

A. Introduction

An understanding of the basis for natural selection and distribution of plants requires knowledge of the physiological basis of adaptation to different natural habitats (Bjoerkman 1981). Because of the widely varying alpine environment the physiological efficiency with which cushion plants adapt to changing conditions may be more important for their survival than performance under optimal conditions. In alpine environments among the most succesful plant species are those which have developed the most appropriate mechanisms for carbon fixation (Pisek et.al.1967, 1969, Billings and Mooney 1968, Dinger and Patten 1974, Moser et al.1977, Schulze 1982).

Carbon dioxide gas exchange measurements of alpine plants have been carried out in laboratories and *in situ* by several authors (e.g.Mooney 1963, Scott and Billings 1964, Mooney et al. 1964, Moser 1969, 1973, Johnson and Caldwell 1974, Grabherr and Cernusca 1977). Since cushion plants are not uniquely suited for investigations of CO_2 gas exchange characteristics and other metabolic activities, they have been relatively neglected by experimental ecologists. Our knowledge of photosynthetic rates of cushion plants is far from complete and scant detailed information is available about underlying environmental responses and adaptive differentiation.

The literature shows that CO_2 gas exchange is influenced by the interactions of many variables both ambient and internal, that is, it responds to the environment as a whole and not to single component factors. These interactions differ among species and environments. However, the characterization of CO_2 gas exchange response of a plant to individual environmental parameters is useful (Mayo et al. 1977).

Photosynthesis is known to depend greatly on the temperature and light conditions under which plants grow (Gloser 1967, Larcher 1969 and 1980, Scott et al. 1970, Moser 1973, Sawada and Miyachi 1974, Grabherr and Cernusca 1977, Kemp et al. 1977, and Bjoerkman 1980). Also, the same temperatures which limit carbon gain can promote carbon loss by accelerating respiration rates.

Since alpine cushion plants receive large amounts of light during their growing season, it can be expected that they are well-adapted to such conditions. Also, extremes of high and low temperatures in dry alpine areas may place special demands on photosynthetic and respiratory abilities of cushion plants. This study investigated the CO_2 gas exchange responses of six cushion plant species to temperature and light intensity in relation to leaf area and dry weight. Possible ecological implications were assessed.

B. Materials and Methods

Carbon Dioxide Gas Exchange

Plant Material

During July 1984, plants utilized in the CO_2 gas exchange study were transplanted from the study site to 10cm diameter pots. All were potted in soils consisting of one part of peat and one part of the alpine soil from the study area on Mt. Allan at an elevation of 2250m asl. Eight to ten mature individuals of each of the six cushion plant species were chosen at uniform size (5 to 10cm surface diameter). Four species, namely *Eriogonum androsaceum*, *Potentilla uniflora*, *Saxifraga caespitosa* and *Saxifraga bronchialis* were transplanted from the southwestern side. The other two species, *Silene acaulis* and *Dryas octopetala*, were transplanted from the northeastern side. The plants were placed in a walk-in growth chamber at the University of Alberta Phytotron.

The growth chamber was programmed for a 14-h photoperiod and a 20°C day/10°C night thermoperiod. Light was provided by white fluorescent tubes supplemented by 20% incandescent bulbs. This gave illumination similar to daylight, except it was somewhat deficient in far red light. Total irradiance at the surface of plants was about 600μmol.m^{-2}.sec^{-1}. Plants were subwatered at weekly intervals by tap water. To allow for adaptation to the pots and restoration of possible root damage in the excavation process, plants were maintained in the growth chamber for about 3 months before running the experiments. At this time all plants possessed leaves which were formed both prior to and during the transplanting period.

Carbon Dioxide Gas Exchange System

Photosynthetic and respiratory CO_2 gas exchange were measured in an open system with an Infra Red Gas Analyzer (IRGA) Beckman model 865. The apparatus and the gas flow circuit are shown in Figure (6.1). The differential method was used in the system, where alternate measurements of the CO_2 concentration were taken from air streams passing over an enclosed plant (sample) and through an empty cuvette (reference).

Ambient air was drawn into the system from the top of the air conditioned laboratory on the seventh floor of the building. The air then passed through a 40x40x20 cm mixing chamber with an inside fan to minimize fluctuations in CO_2 concentration. The drawn air passed through silica-gel before it was pumped into the system. The air was then split into two streams of an uniform flow rate of 1 liter/min using an auxilliary pump. One stream was routed through the reference cell, and the other stream was routed to the cuvettes and the sample cell of the IRGA. A blank chamber (volume

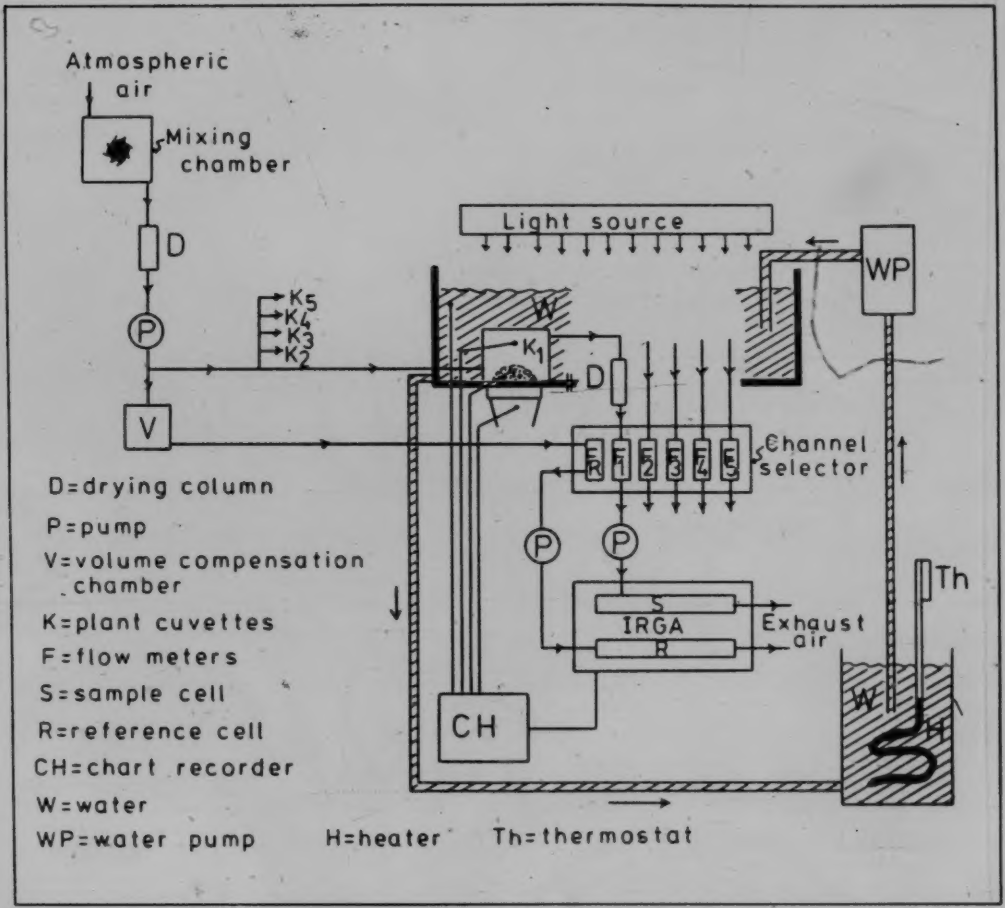

Atmospheric air
Mixing chamber
D
P
K5
K4
K3
K2
V
Light source
WP
W
K1
D
F R
F 1
F 2
F 3
F 4
F 5
Channel selector
P
P
S
IRGA
R
Exhaust air
Th
W
H
CH
D=drying column
P=pump
V=volume compensation chamber
K=plant cuvettes
F=flow meters
S=sample cell
R=reference cell
CH=chart recorder
W=water
WP=water pump
H=heater
Th=thermostat

Figure (6.1): Diagram of the IRGA system.

compensation chamber) in the reference air stream with volume equal to that of the cuvettes in the sample stream removed effects of short-term fluctuations in CO_2 concentration of the outside air. Ambient CO_2 concentration was monitored by comparison to standard gases, and CO_2 depletion in the cuvette was adjusted so that in the cuvette the concentration was in the 325 to 395 ppm range. Air entered the shoot cuvettes (shoot compartments) from the bottom through 1/2 inch plastic tubing, and was withdrawn from the top, ensuring mixing of the air in the cuvette. The humid air was pumped out of the shoot cuvettes, passing through a desiccating column of silica-gel and then pumped into the sample cell of the IRGA. The shoot cuvettes were cylindrical and made of plexiglass with 12 cm diameter and 10 cm depth (Volume 1.13 liter).

An automatic multichannel selector connected each of the 6 cuvettes for one minute with the IRGA in rotating mode, allowing for a recording of CO_2 concentration in each cuvette every 6 minutes. Copper-constantan thermocouples were used to monitor leaf and air temperatures inside the cuvettes. The thermocouple sensors were also connected to the chart recorder. The temperature of the circulating water bath around the cuvettes was maintained by a heater (controlled by a thermostat) to give any required temperature above 20°C. Temperatures lower than 20°C were attained by adding crushed ice to the water reservoir, and for temperatures around 0°C ice and salt were put around the cuvettes. Light was provided by H.I.D. lamps. The two lamps were held on a vertical adjustable assembly calibrated for varied height levels. Irradiance (μmol.m^{-2}.sec^{-1}) inside the shoot cuvettes was monitored by a Licor Quantum radiometer (Model LI-185). The temperature in the cuvettes was held constant at 22.7°C ± 1.6°C.

Experimental Procedure

Plants were watered 24 hours prior to the experiment. The whole potted plant was placed upon specially buffered stands with its tops fitted to the base of the cuvettes. The pots were sealed into the bottom of the shoot cuvette with Terostat sealing compound and were left in the dark overnight. The following day, measurements were made after the plants had equilibrated to the airflow and temperature conditions, i.e., after steady-state levels were achieved. The general procedure for analysis of the effect of temperature and light intensity on CO_2 gas exchange was to maintain the plants at a constant temperature or light intensity until stable measurements were achieved (from 10 to 15 min.). Then, the treatment was gradually changed. The desired leaf temperatures were obtained by adjusting the temperature of the water bath. The temperature was changed from low to high degrees. The temperature of the soil was independent of that of the shoot cuvette (18±3 °C). Light intensity was varied by altering the height of the two lamps over the cuvettes one or two at a time. Approximately five hours elapsed between the initiation of an experiment and its completion.

After net photosynthesis had been determined, the light was turned off and the cuvettes were covered with a black cloth, and dark respiration was determined under different temperatures. The effect of temperature on CO_2 gas exchange was measured on one set of plants, the effect of light intensities was measured on another set. To minimize the influence of soil respiration the air in the cuvettes was kept under slight pressure (monitored on a little balloon). In addition, the CO_2 contribution to the cuvette from the soil was measured after cutting the green leaves off the shoots. After each experiment, the actual leaf area (one side) was determined by xeroxing the leaves on transparencies, and passing these through the leaf area meter. Oven dry weight determinations were made after allowing the leaf sample to dry at 80°C for 24 hours. CO_2 gas exchange rates were expressed on the basis of the actual "one-surface" leaf area (mg $CO_2.dm^{-2}.h^{-1}$) and per unit leaf dry weight (mg $CO_2.g^{-1}DW.h^{-1}$). The results given are averages for three plants per species.

Calculation of the Results

The differential in CO_2 concentration between incoming ambient air and air stream withdrawn from the cuvette (Δ CO_2) provided a measure of photosynthetic and dark respiration rates. The amount of soil respiration was added to Δ CO_2 in the case of photosynthesis, and subtracted from dark respiration. The net gain or loss of CO_2 was calculated according to the formula:

mg $CO_2.g^{-1}DW.h^{-1} = \Delta .0{,}00184.60.\mathrm{calibration}.g^{-1}DW$

where DW = dryweight of leaves

(1 l CO_2 = 1840 mg at 20°C, at 0°C or lower a value of 1977 mg was used).

Leaf Area Index (LAI)

Plant material was sampled for determination of the leaf area index (m^2 leaf area per m^2 cushion plant surface) at the peak season (flowering/fruiting stage) of 1983 from the sites on Mt. Allan. Three plants with uniform intermediate size (per species) were chosen. The entire range of leaf shapes of the species, representing a scale of leaf sizes from those which had just unfolded from the bud to fully expanded leaves, was placed on graph paper and their margins were outlined (silhouettes). The area of every outlined leaf was determined by counting the mm^2 within the outline. The leaves were then sorted into different leaf area classes: less than 5 to 5, 6 to 10, 11 - 20, 21 - 40, 41 - 80 mm^2, etc. Leaves that fell between two area classes were grouped with the lower one. By using the rating method (Sestak et al. 1971), the area of every leaf of an individual plant was rated according to its similarity to a member of the appropriate silhouette. The area of every leaf area class and eventually the total leaf area were calculated. This procedure was fairly rapid and well suited for determining the LAI of cushion plants.

C. Results

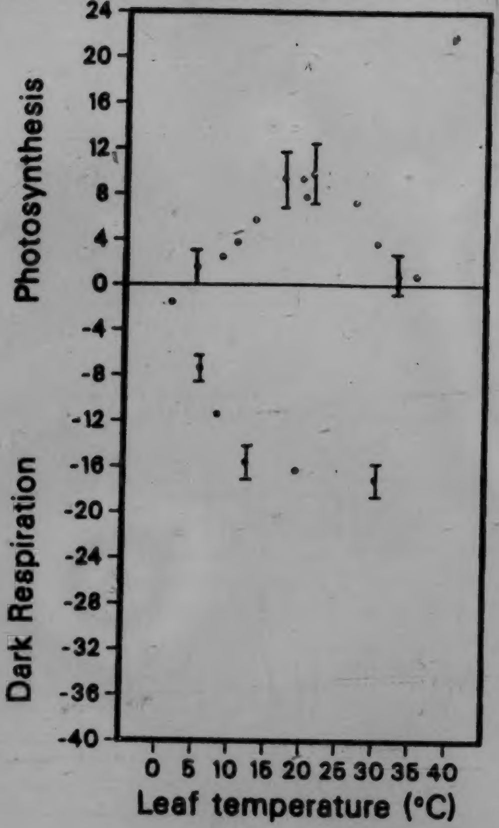
Effect of Temperature

Rates of net photosynthesis for whole plants were measured at various leaf temperatures from about 0 to 40°C with constant irradiation of about $460\mu mol.m^{-2}.sec^{-1}$. Dark respiration rates were determined at the same range of temperatures (Appendix 12). The general relationship between net photosynthesis and leaf temperature was similar in most of the species investigated, with only small differences in temperature minima, optima, and maxima.

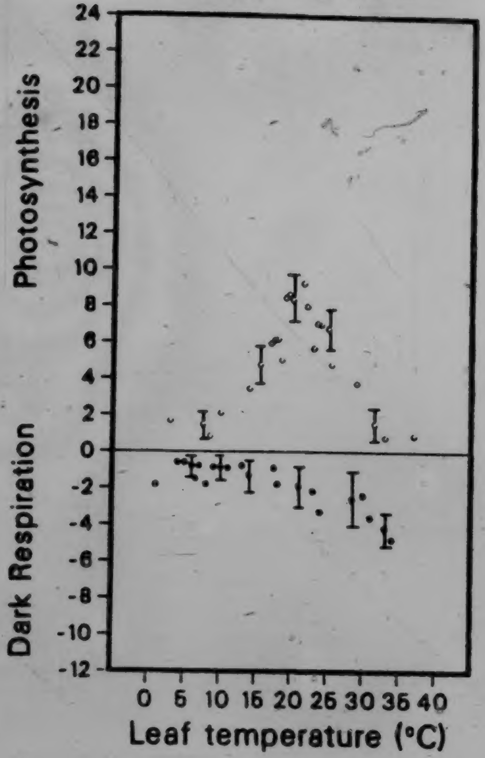
In *E. androsaceum* and *P. uniflora*, net photosynthesis increased rapidly with temperature up to the optimum temperature (about 21°C), then decreased until it reached about 10% at 35°C for both species (Fig.6.2). The highest photosynthetic rates attained by the two species were about 10 and 9 mg $CO_2.g^{-1}DW.h^{-1}$. The minimum temperature of positive net CO_2 fixation for the two species was 2°C.

0

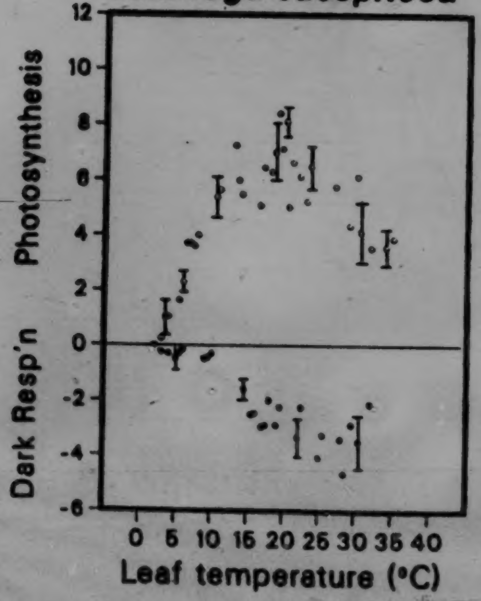
Figure (6.2): Effect of leaf temperature (°C) on net photosynthesis at 460μmol.m^{-2}.sec^{-1}, and dark respiration of the different species.



Eriogonum androsaceum



Potentilla uniflora



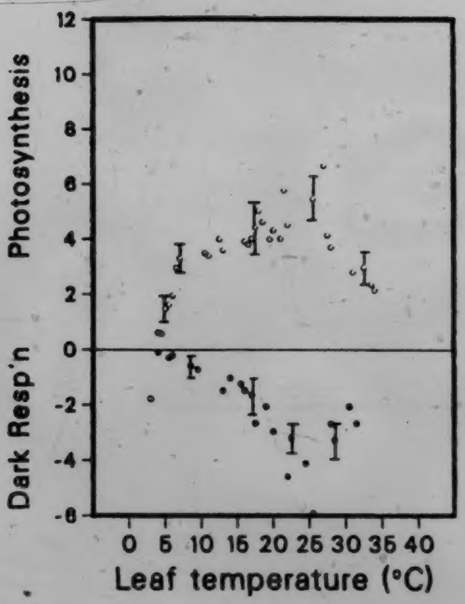
Saxifraga caespitosa

Photosynthesis

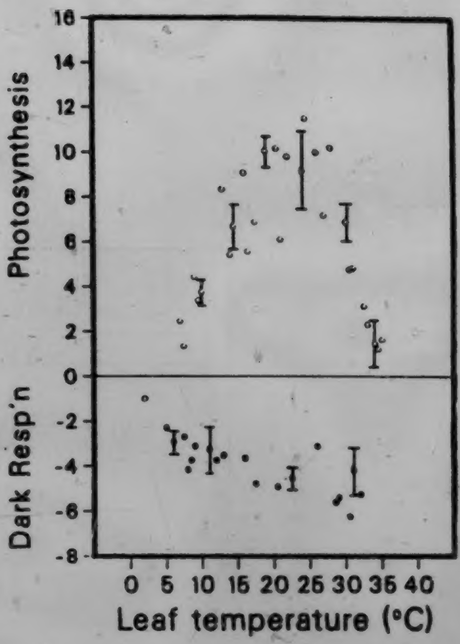
mg $CO_2 \cdot g^{-1}$ $Dw \cdot h^{-1}$

Dark Respiration

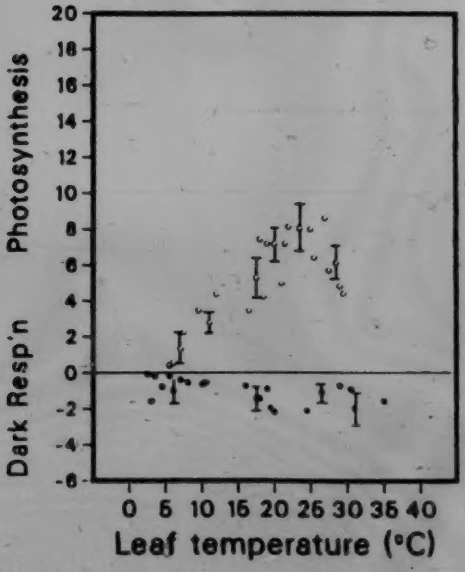
mg $CO_2 \cdot g^{-1}$ $Dw \cdot h^{-1}$



Saxifraga bronchialis



Silene acaulis



Dryas octopetala

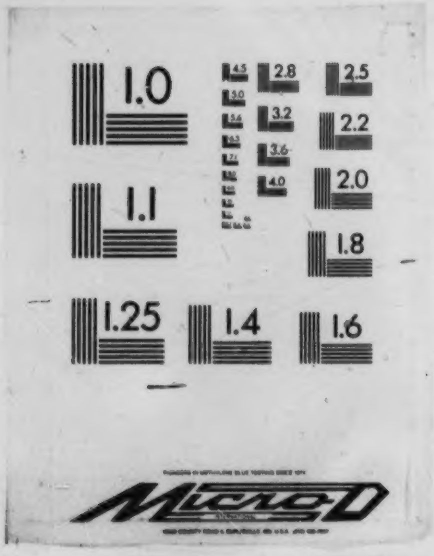
Photosynthesis

mg $CO_2 \cdot g^{-1}$ Dw·h^{-1}

Dark Respiration

mg $CO_2 \cdot g^{-1}$ Dw·h^{-1}

3


1.0
4.5
5.0
5.6
2.8
3.2
3.6
4.0
2.5
2.2
2.0
1.1
1.8
1.25
1.4
1.6
MicroD

The photosynthetic rates of *Saxifraga caespitosa* and *Saxifraga bronchialis* responded linearly to leaf temperature up to about 10°C, then the curves levelled off over a range from 15°C to 25°C, then photosynthetic rates decreased. At 35°C *S. caespitosa* still showed 45% (*S. bronchialis* 30%) of maximal activity. The minimum temperature of positive net CO_2 fixation for the two species was 2.5°C, while the optimum temperatures were around 20°C and 25°C, respectively. The maximum photosynthetic rates attained by the two species were about 8 and 6 mg $CO_2.g^{-1}DW.h^{-1}$, respectively.

For *Silene acaulis* and *Dryas octopetala*, the curves of photosynthesis as a function of leaf temperature increased almost linearly up to the optimum temperature (around 25°C) where the highest photosynthetic rates were reached (about 11 and 8 mg $CO_2.g^{-1}DW.h^{-1}$). Then, the rate declined sharply till it reached about 10% and 22% of the maximum at 35°C and 30°C, respectively. The minimum temperatures of positive net CO_2 fixation were 3°C and 4°C, respectively.

Plant species widely distributed on the NE side (*D. octopetala* and *S. acaulis*) possess higher minimum and optimum temperatures for photosynthesis than the species distributed on the SW side, such as *Eriogonum androsaceum* and *Potentilla uniflora*. The two *Saxifraga* species, which are associated with exposed microsites among rock crevices and outcrops, have the upper limits of net photosynthesis at higher leaf temperature.

All the species studied exhibited an increase in dark respiration with increasing temperature, thereby reducing net assimilation. *E. androsaceum* has the highest dark respiration rate among the studied species (overall average 13.44±3.63 mg CO_2 . g^{-1}DW . h^{-1}). In the remaining species the average values ranged from 1.03±0.67 mg CO_2 . g^{-1}DW . h^{-1} in *Dryas octopetala* to 4.10±1.10 mg CO_2 . g^{-1}DW . h^{-1} in *Silene acaulis*.

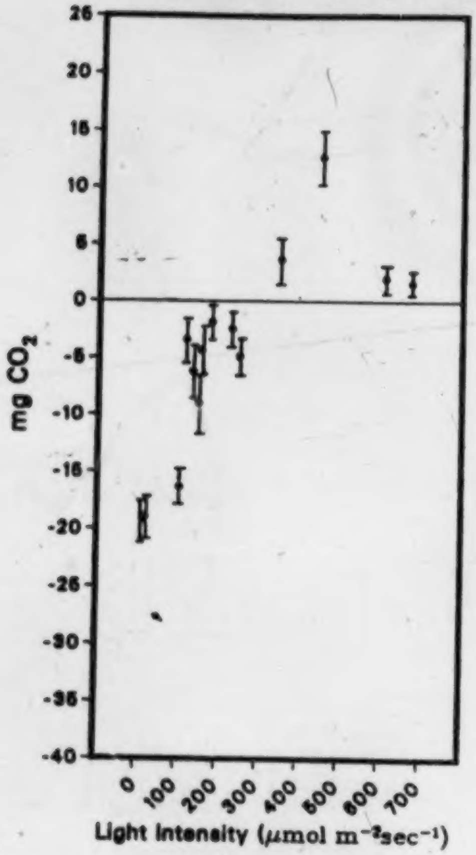
Effect of Light

The dependence of CO_2 exchange on light intensity has the character of a saturation curve with a rapid increase in photosynthesis at low light intensities. There were large differences between species in their response to light intensities (Appendix 13). *P. uniflora* and *S. acaulis* showed increasing rates up to the highest light intensity used, while photosynthesis in *S. bronchialis* leveled off at about 250 μmol.m^{-2}.sec^{-1}. The remaining three species showed a decrease of photosynthesis at the highest light intensities used (Fig.6.3).

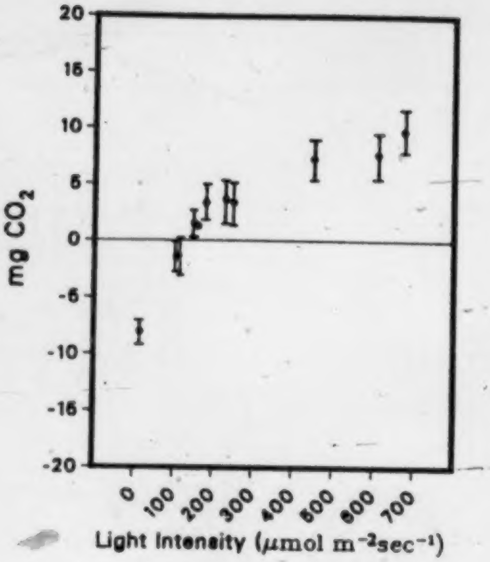
The light compensation points of *S. caespitosa*, *S. bronchialis* and *D. octopetala* were approximately 80μmol.m^{-2}.sec^{-1}. Light compensation points of *E. androsaceum* and *S. acaulis* were 270 and 140 μmol.m^{-2}.sec^{-1} respectively, while their light saturation point was as high as 450 μmol.m^{-2}.sec^{-1}. *P. uniflora* possesses an intermediate light compensation point of 140 μmol.m^{-2}.sec^{-1};

0

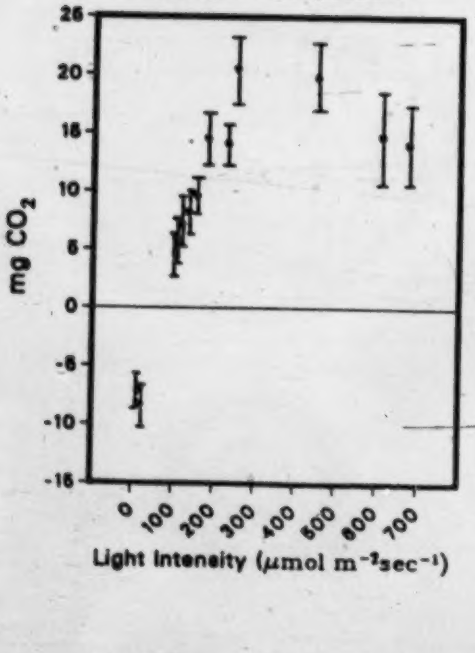
Figure (6.3): Effect of light intensity on net photosynthesis at constant temperature (22.7 ± 1.6°C) of the different species.



Eriogonum androsaceum

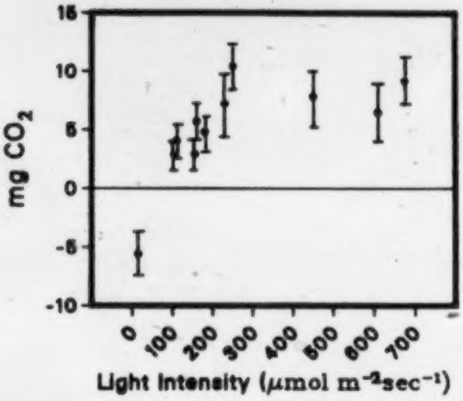


Potentilla uniflora

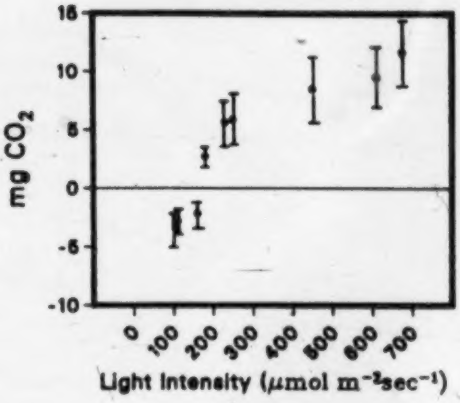


Saxifraga caespitosa

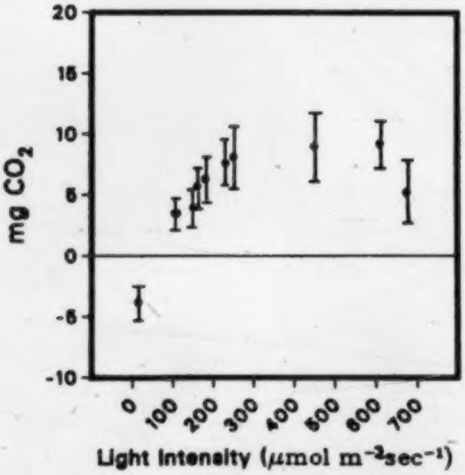
mg $CO_2 \cdot g^{-1}$ $Dw \cdot h^{-1}$



Saxifraga bronchialis



Silene acaulis



Dryas octopetala

mg $CO_2 \cdot g^{-1}$ Dw$\cdot h^{-1}$

unlike the other species it was not light saturated at 650 $\mu mol.m^{-2}.sec^{-1}$.

Plant species on the SW side seem to need higher light intensity for saturation and higher light compensation points than the species on the NE side.

Leaf Area Index

The variation of LAI's between species was very high. The total LAI's ranged from 0.68 in *S. acaulis* at the crest to 6.14 in *E. androsaceum* on the upper slope. There was no apparent trend in total LAI's of the different species with site (Table 6.1). However, the total LAI of *S. acaulis* and *D. octopetala* declined significantly at the crest site in response to human impact. Trampling by many recreationists destroyed many plants in this area. The total LAI of *E. androsaceum* on the upper slope was higher than on the lower slope and ridge, while *P. uniflora* attained total LAI on the lower slope slightly above the values at the two other sites. The two species *E. androsaceum* and *S. bronchialis* have the highest total LAI's among the species investigated, and *P. uniflora* has the lowest total LAI; its values ranged from 1.37 on the upper slope to 1.83 on the lower slope.

Each individual rosette on top of each shoot in a cushion consists of a number of green leaves increasing in age from the inner leaves of the rosette which had just unfolded (youngest) to the next expanded leaves

Table (6.1) Leaf area indices (m^2 leaf area per m^2 cushion surface) for different leaf area classes of the six species at various sites of the study area.

Species	Leaf area class(mm)	SW-side			Crest	NE-side
		Lower slope	Upper slope	Ridge		
E.androsaceum	< 5	0.05	0.14	0.14		
	6- 10	0.16	0.59	0.68		
	11- 20	1.00	1.35	1.23		
	21- 40	1.33	2.13	2.01		
	41- 80	1.28	1.58	1.03		
	81-160	0.46	0.35	0.06		
	total	4.28	6.14	5.15		
P.uniflora	< 5	0.12	0.08	0.08		
	6- 10	0.18	0.16	0.14		
	11- 20	0.02	0.10	0.08		
	21- 40	0.53	0.27	0.60		
	41- 80	0.67	0.62	0.61		
	81-160	0.21	0.11	0.07		
	161-320	0.10	0.03	0.00		
	total	1.83	1.37	1.58		
S.caespitosa	< 5			0.06		
	6- 10			0.26		
	11- 20			0.73		
	21- 40			0.95		
	41- 80			0.23		
	total			2.23		
S.bronchialis	< 5			0.32		0.31
	6- 10			2.18		1.46
	11- 20			3.21		2.84
	21- 40			0.34		0.61
	total			6.05		5.22
S.acaulis	<5			0.28	0.09	0.11
	6- 10			1.36	0.42	0.92
	11- 20			0.71	0.17	0.96
	21- 40			0.30	0.00	0.58
	total			2.65	0.68	2.57
D.octopetala	< 5				0.02	0.01
	6- 10				0.09	0.02
	11- 20				0.25	0.17
	21- 40				0.35	0.27
	41- 80				0.14	0.55
	81-160				0.10	0.72
	161-320				0.00	0.52
	total				0.95	2.23

(medium aged) which occur outside the inner immature leaves, followed by the oldest green leaves. These green leaves are followed by dead leaves still attached to the stem. More than half of the total LAI's was accounted for by the medium-aged leaf area classes.

Some observation of green leaf inclinations shows the erectophilic nature of most of the cushion plant leaves. However, the leaf angles were not measured. The green leaves of the two *Saxifraga* species tended to be inclined more toward the stem axis (steeply inclined) than leaves of the other species.

In both temperature and light experiments, the net photosynthesis rates based on leaf area (App.12) were about twice the rates based on leaf dry weights in *Eriogonum androsaceum*, *Potentilla uniflora* and *Dryas octopetala*. In the remaining species, the net photosynthesis rates were only a little higher on leaf are basis than on dry weight basis.

D. Discussion

The CO_2 gas exchange measurements were taken at a series of artificially varied leaf temperatures and light intensities using an infrared gas analyzer (IRGA). The rates of net photosynthesis are rather low when compared with other groups of plants (Wolf 1969), while the rates of respiration are high. The poor photosynthetic performance and very high respiration rate of *E. androsaceum* under tested conditions are not fully understood.

Many alpine plants photosynthesize at temperatures as low as -5°C, while the optimum temperature may vary between 8 and 22°C (Mooney 1963, Tranquillini 1964, Billings 1974, Moser 1973, Mark 1975, Moser et al. 1977). The maximum temperature where zero CO_2 gas exchange occurs is usually 35°C or a little above for most alpine species (Bliss 1962, Billings et al. 1966, Billings and Mooney 1968, Pisek et al. 1969). Parkhurst and Loucks (1972) generalized that in arctic and alpine regions, those plant species whose carbohydrate metabolism is most severely limited by low temperatures, are most likely to evolve a cushion form of growth. The present study shows that alpine cushion plants from Mt. Allan with a minimum photosynthetic temperature between 2 and 4°C, an optimum temperature between 21 and 25°~~C~~ and maxima above 35°C are not in common with many other alpine plants (Table 6.2). In addition the temperature requirements differed considerably from temperature characteristics of other cushion plants. Moser et al. (1977) found temperature optima in *Saxifraga bryoides* and *S. moschata*, measured *in situ* at 3184 m asl, between 15 and 20°C. In agreement with Mawson et.al. (1986), the high temperature optima for photosynthesis in the six species studied can be partially attributed to acclimation to higher growth temperatures (20/10°C day and night respectively).

Table (6.2): Photosynthetic characteristics of the six species investigated.

	Species					
	ERAN	**POUN**	**SIAC**	**SACA**	**SABR**	**DROC**
Light compen. point (μ mol/m^2/sec)	270	140	140	80	80	80
Light satur. point	450	>650	450	250	250	250
Min. temp. (°C)	2.0	2.0	2.0	2.5	2.5	4.0
Max. temp. (°C)	>35	>35	>35	>35	>35	>35
Opt. temp. (°C)	21	21	25	20	25	25
Photosyn.at opt.temp. (mg CO$_2$/gDW/h)	10	9	11	8	6	8
Overall average resp. (mgCo$_2$/gDW/h)	13	2	4	2	2	1

Fischer and Kuhn (1984) have presented excellent measurements of diurnal leaf temperatures of cushion plants in northern Sweden. The values of leaf temperature were above those of the ambient air. Also, leaves of mountain plants under intense solar radiation may have high temperatures, up to 15 to 20°C above the ambient air (Tranquillini and Turner 1961, Salisbury and Spomer 1964, Billings et al. 1966, Larcher 1977). These findings agree with the data presented in chapter two of this study. Physiological processes will be continued even when air temperatures are low (Berry 1975). This gives the plants a longer period of adequate growing conditions (Addison 1977, Grabherr and Cernusca 1977, Fischer and Kuhn 1984). The microclimatic conditions within the cushion plant canopy are more favourable than the ambient climate.

The investigated species have either small scale-like, entire and relatively large, or divided leaves. Theoretically, the divided and large leaves are more efficient in losing heat to the environment than small simple leaves (Billings et al. 1966). The leaves of *P. uniflora* and *S. caespitosa* are of the latter type, while *E. androsaceum* leaves are entire and relatively large. These morphological features may be involved in the maintenance of positive net photosynthesis, where the above-mentioned three species have lower optimum temperature than the other species.

The rates of dark respiration were high, probably due to the high concentrations of soluble carbohydrates, which have been found for plants in cold regions (Wager 1941, Pisek 1960, Mooney and Billings 1960 and 1961, Billings 1974, Moser et al. 1977, Hadley and Bliss 1964), or due to high leaf temperatures or both (Salisbury and Spomer 1964, Mayo et al. 1977, Fischer and Kuhn 1984). This could allow the respiration rates to exceed photosynthesis rates at least for short periods, resulting in net photosynthesis dropping below the compensation point despite adequate illumination. Since respiration rates increase exponentially with temperature, plants with a low assimilation rate may be starved by high temperature. This has been observed on mountain plants transplanted to the lowlands with warm night temperatures. Generally, net photosynthesis is relatively low because of high respiratory rates (Bate and Smith 1983).

Most alpine and arctic species have light compensation points from 36 to 92 μmol.m^{-2}.sec^{-1} at 15°C and 20°C (Scott and Menalda 1970, and Tieszen 1973, Karlsson 1985). The light compensation points of cushion plants at about 23°C leaf temperature are in the range of 80 to 270 μmol.m^{-2}.sec^{-1}.

Many arctic and alpine species exhibit light saturation in the range of 170 to 500 μmol.m^{-2}.sec^{-1} (Mueller 1928, Wager 1941, Mooney and Billings 1961, Hadley and Bliss 1964, Kuramoto and Bliss 1970, Moser 1973, Mark 1975, Skre 1975, and Mayo et al. 1973 and 1977). However, Scott and Billings

(1964) reported that several alpine species did not achieve light saturation at about 1880 μmol.m^{-2}.sec^{-1}. Schulze (1979) pointed out, that at low temperatures photosynthesis becomes susceptible to high light which causes photo-inhibition. This effect together with chlorophyll destruction under increased UV light, causes a decrease in photosynthesis at high elevations. The light saturation levels for most cushion plants on Mount Allan are in the range from 250 to 450 μmol.m^{-2}.sec^{-1}, with the exception of *P. uniflora* which did not achieve light saturation at 650 μmol.m^{-2}.sec^{-1}. Self-shading reduces the light intensities for the older set of leaves. The leaf self-shading mechanism enables cushion plants in their open habitats with abundant light to adjust to the efficient use of high light intensities which might be damaging to their photosynthetic apparatus. Grabherr and Cernusca (1977) compared the photosynthetic capacity of unshaded leaves with that of the average leaf layer within the canopy of the cushion plant *Loiseleuria procumbens*. They found that saturation of unshaded leaves was reached at higher irradiance than with leaves from within the canopy. Ross (1970) showed that saturation by irradiance is achieved only in plant communities with horizontal leaves and not with predominantly vertical leaf inclination. This indicates that leaves shaded by other leaves of the same plant experience limitations similar to those experienced by a plant shaded by other plants.

Considering the concept of "sun" and "shade" plants, the "sun" type has a high rate of maximal assimilation, a high rate of respiration and in consequence a relatively high light intensity at the compensation and saturation points. The "shade" plant has the reverse in each instance. In cushion plants as in many other plants the leaves on the same ind the leaves on the same individual plant may have differing light response characteristics because of branch geometry and leaf self-shading. In alpine areas, cushion plants should be regarded as "sun" plants since there is no shade from other plants, yet even so, the species investigated show a similar range in CO_2 assimilation as plants described as "sun" and "shade" types in other regions. Accordingly, the species investigated can be grouped into two types: 1) Plants with high light requirements. They orient their leaves (at least the older leaves) nearly at a right angle to the radiation (e.g. *Eriogonum androsaceum*, *Potentilla uniflora* and *Silene acaulis*). 2) Plants with low light requirements. They orient leaf edges to the sun which minimizes their radiation load advantageously in these alpine conditions of high radiation intensity (e.g. *Saxifraga caespitosa*, *Saxifraga bronchialis* and *Dryas octopetala*.)

With respect to the relationship between LAI and CO_2 gas exchange, *E. androsaceum* and *S. bronchialis* with high LAI's are characterized by lower photosynthetic rates, while those species with lower LAI's (*P. uniflora* and *D.*

octopetala) had relatively high photosynthetic rates. This may be seen as a result of the sheltering and self-shading of leaves, but also of increased average leaf age with higher LAI. Pearce et al. (1965) found that for every LAI unit added to the stand over the LAI range of 3 to 8, leaf efficiency dropped by 0.76 mg CO_2 g^{-1}DW.h^{-1}, while at low leaf areas, each LAI unit adds significantly to net photosynthesis. Studies with models (Duncan et al. 1967, Anderson and Denmead 1969, and Duncan 1971) have shown that for high LAI's, photosynthetic efficiency is greater with more erect leaves. The more vertical the leaves the more efficient they are at utilizing light energy. Therefore, the erectophilic nature of some cushion plant leaves seems to be an adaptive mechanism to improve its photosynthetic efficiency. Pearce et al. (1967) have shown that vertical leaves had higher net photosynthesis and allowed more light to penetrate at high LAI's than horizontal (perpendicular to the light source) leaves. The advantage of horizontal leaves is lost at high LAI's because of increased mutual shading. Based on these results and the findings of other investigators, leaf area is probably a critical factor, particularly during the early part of the growing season when leaf area is low and moisture is available.

E. Species Distribution

It is interesting to consider whether the results so far give any indication of the factors that lead to the distribution of alpine cushion plants. Why is one species eliminated from a particular habitat while others survive?

In comparing assimilation rates for the six species investigated, it is apparent that species segregation exists with respect to CO_2 assimilation.

Johnson and Caldwell (1975), Bunce et al.(1979) found that wider-ranging species have apparently evolved mechanisms which contribute to high photosynthetic rates under prevailing alpine environments. This is in contrast to narrower-ranging species which appear to have lower photosynthetic rates.

In the present investigation, the species with similar distributions have similar photosynthetic responses to both temperature and light. An important difference between widely and narrowly-distributed species are the high light compensation and light saturation points in widely distributed species. The wide-ranging species have also lower temperature optima and minima, even though, photosynthetic rates of the two *Saxifraga* species (restricted distribution) are not as high as for other species under the tested temperature conditions. These two species are able to maintain positive net photosynthesis over a wider range of temperature regimes. Therefore, the attainment of low or high temperature requirements for assimilation is considered an important factor in the distribution of alpine cushion plant species.

F. Summary

The findings of this study can be summarized as follows:

1. The rates of CO_2 gas exchange in response to temperature and light were measured on six cushion plant species by using an infrared gas analyzer. Plants exhibited differences in their photosynthesis and respiration characteristics in ways apparently reflecting the temperature and light regimes of their native habitats.
2. Net photosynthesis was rather low, while the rate of dark respiration was relatively high. The low net photosynthetic rates may have been related to increased respiration, leaf clustering and mutual shading, and increased leaf area index, thus masking the true leaf efficiency. There may also be effects of soil respiration.
3. Cushion plants are not in common with many other alpine plants, with their minimum photosynthetic leaf temperature between 2 and 4°C, optimum temperatures 21 to 25°C, and maximum temperatures above 35°C .
4. The light compensation values for some cushion plants at about 23°C leaf temperature are higher than for other alpine plants. They are in the range from 80 to 270 $\mu mol.m^{-2}.sec^{-1}$, while the light saturation values stay

in an intermediate range of 250 to 450 μmol.m^{-2}.sec^{-1}.

5. The microclimate conditions within the cushion plant canopies are more favourable than the ambient climate. This gives the plants a longer period of adequate growing conditions. That is, CO_2 exchange processes are expected to be active when air temperatures are low.
6. Leaf self-shading and orientation, and branch geometry enable cushion plants in their open habitats with abundant light to adjust to the efficient use of high light intensities, avoiding damage to their photosynthetic apparatus.
7. Species with high LAI's are characterized by reduced photosynthetic rates, while those with lower LAI's have relatively high photosynthetic rates. This can be viewed as a result of leaf self-shading and increased average leaf age with higher LAI's. With high LAI, the oldest active leaves in each rosette may have slightly positive or even negative carbon balance on average over the day.
8. The different responses of cushion plants to temperature and light is one contributing factor in determining the local distributions of the studied species in alpine areas.

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VII. Resource Allocation

A. Introduction

An important aspect of the reproductive strategies of plants is the allocation of resources to various organs or functions within an individual (Harper 1967, Silvertown 1982). In severe environments plant growth-forms are often considered important features of ecological studies (Grulke and Bliss 1985), while reproductive strategies have become a central concept in theories of life history evolution (Hirschfield and Finkle 1975).

According to Mooney and Chu (1974) resource allocation patterns to growth, storage, maintenance, and protection likely represent the means by which plants meet the demands of their environment. These patterns, although difficult to follow (Harper 1977), have been shown to vary both within and between species (Grime 1979, Soule and Werner 1981, Abrahamson and Caswell 1982). Variation in resource allocation among populations may arise from genotypic differences, phenotypic plasticity, environmental effects, or a combination thereof (Hickman 1975, McNaughton 1973, Andel and Vera 1977, Cartica and Quinn (1982). Patterns of reproductive allocation differ in different habitats. Asexual reproduction is believed to be more important with an increase in environmental severity and more unpredictable environments. Plants of early successional stages typically allocate a larger proportion of biomass to sexual reproduction, those in more mature systems allocate a lesser amount (Gadgil and Solbrig 1972, Gaines et al.1974, Werner 1976, Holler and Abrahamson 1977, Abrahamson 1979, Seischab et al.1985). The implications of the patterns of energy allocation and reproductive capacity have been interpreted in terms of the concept of adaptive strategy (Harper 1967, Abrahamson and Gadgil 1973, Cody 1974, Kawano 1981, Thompson and Stewart 1981, Sano and Morishima 1982, Kawano and Miyake 1983, Maessen et al.1983, Kaul 1985).

Within a single growing season alpine plants have a limited amount of time, matter and energy available to devote to growth, maintenance and reproduction. The way in which they allocate these resources is of fundamental importance to their survival. The fact that some cushion plant species have a wide range of altitudinal distribution while others are restricted to certain localities suggests that the widely distributed species have optimized the partitioning of resources in a way that maximizes fitness.

Harper and Ogden (1970) introduced a method of studying energy allocation in plants which requires separation of the tissues according to their function and the expression of the energy allocation as the proportion of the biomass stored in each tissue type. Many authors have used this method since (Hickman and Pitelka 1975, Roos and Quinn 1977, Newell and Tramer 1978, Bostock and Benton 1979, Bostock 1980, Boutton et al.1980, Douglas 1981, Kawano 1981, Stewart and Thompson 1982, Wigham 1984 etc.). The purpose of this study was to investigate alpine cushion plant reproductive strategies and to compare the resource allocation patterns of six species at various sites in their natural habitat. The role of some local factors such as wind, run-off, solifluction and animal life on vegetative reproduction will be discussed.

B. Material and Methods

Six species of cushion plants were harvested at the study site on Mount Allan between 2100 and 2380 m asl: *Eriogonum androsaceum* Benth., *Potentilla uniflora* Ledeb., *Saxifraga caespitosa* L., *Saxifraga bronchialis* L., *Silene acaulis* L., and *Dryas octopetala* L. ssp. *Hookeriana.*

When flowering reached its peak five individuals of each species per site were collected at random sample points, placed into plastic bags and processed in the laboratory within 10 hours after harvesting. Due to the extensive root systems and difficult terrain the excavating of each single plant was time consuming (up to 6 hours per individual) but almost all of the belowground biomass was collected. The soil was washed out in the laboratory, the dead organic matter, forming the "packing material", was separated visually. The plant components were sorted into vegetative organs (roots, stems, leaves) and sexual reproductive tissue (flower buds, flowers, pedicels, peduncles, fruits). The material was then dried in an oven for 48 hours at 80°C. The dry weight of each compartment was expressed as percentage of the total dry weight of each individual.

The vegetative reproductive allocation (VRA = dry weight of vegetative organs/dry weight of total biomass of individual), and the sexual reproductive allocation (SRA = dry weight of the sexual structures/dry weight of total biomass of individual) were calculated for each species. Since leaves represent resources accumulated during one or two growing seasons, i.e., not perennating organs, they were excluded from the calculation of VRA. Therefore the total percentage of SRA plus VRA is not equal to 100%.

Ideally RA should be measured in terms of energy rather than biomass, but Hickman and Pitelka (1975) noted that energy content and dry weight measures equally reflect energy allocation patterns. A one-way ANOVA was done to determine if there were significant differences among sites. The study was conducted during the growing season of 1984.

C. Results

Phytomass Distribution

Dry matter distribution to various plant components expressed as percentage of the total phytomass for each of the six species studied are given in Table (7.1). The allocation of the total phytomass to the various tissues differed at the time of harvest as follows:

In *Eriogonum androsaceum* and *Saxifraga bronchialis* the largest proportion was present in the roots, while *Potentilla uniflora*, *Saxifraga caespitosa*, and *Dryas octopetala* allocated the largest proportions to their stems. In contrast *Silene acaulis* allocated more of its phytomass to the leaves. All species studied showed the least phytomass allocation to the flowers.

The comparison between sites indicates that in all species the average percentage of phytomass present in roots varied significantly (at 95% probability) among sites except *S. acaulis* which did not show significant differences. The percentage of root dry matter in *E. androsaceum* increased from 39% at the lower slope to 50% at the ridge, while in *P. uniflora* the range was from 26% at the crest to 38% at the lower slope. *S. bronchialis* showed the highest dry matter partitioning to its roots at the north-east site (55 %) which decreased to 44 % at the ridge. The opposite is true for *S. acaulis* where the range increased from 26 % at the north-east site to 29% at the ridge. *D. octopetala* allocated 33% of its dry weight to roots at the north-east side of the study area and 36% at the crest.

The average percent dry matter distributed to stems of *E. androsaceum* showed no significant difference between sites, while the material allocated to the stems of *P. uniflora* was significantly different at the lower slope from the plants at the ridge and at the crest.

Table (7.1) The average percentage of total live dry matter components in the different species at various sites of the study area. Standard deviation in parentheses. Underlined numbers in different columns showed non-significant differences among sites. (5 plants/species/site)

Species and plant organ	South-west side		Upper Crest	North-east side
	Lower slope	Ridge		
Eriogonum androsaceum				
Root	39(08.3)	50(11.8)	46(09.5)	
Stem	32(06.5)	31(08.5)	31(10.3)	
Leaf	21(05.7)	14(04.5)	18(05.2)	
Flower	08(02.6)	05(01.8)	05(02.0)	
Potentilla uniflora				
Root	38(15.5)	34(12.4)	26(10.4)	
Stem	43(14.0)	50(16.4)	53(14.6)	
Leaf	14(04.4)	14(05.0)	16(05.3)	
Flower	05(02.6)	02(01.3)	05(01.0)	
Saxifraga caespitosa				
Root		32(10.6)		
Stem		38(12.0)		
Leaf		15(06.4)		
Flower		15(08.3)		
Saxifraga bronchialis				
Root		44(07.2)	48(10.6)	55(09.8)
Stem		40(10.6)	42(12.5)	34(07.4)
Leaf		11(06.8)	07(03.6)	08(04.2)
Flower		05(02.5)	03(01.4)	03(01.0)
Silene acaulis				
Root		29(13.0)		26(11.2)
Stem		22(07.5)		26(08.0)
Leaf		42(05.6)		40(05.0)
Flower		07(02.4)		08(03.3)
Dryas octopetala				
Root			36(09.0)	33(07.5)
Stem			50(11.4)	50(13.8)
Leaf			13(05.2)	13(07.0)
Flower			01(00.5)	04(01.5)

At the north-east site and the ridge both *Saxifraga bronchialis* and *Silene acaulis* showed significant differences between sites. *Eriogonum androsaceum* showed a significant difference between sites in dry matter allocation to its leaves. The average percentage of leaf dry matter of *E. androsaceum* was 21% at the lower slope and 14% at the ridge, while the leaves at the crest attained 18%. *S. bronchialis* showed a significant difference between leaf samples taken from the ridge and the north-east site.

In contrast to *S. bronchialis*, the two species *S. acaulis* and *D. octopetala* attained significant differences between sites in dry matter allocation to flowers, while *E. androsaceum* and *P. uniflora* showed significant differences between ridge and lower slope sites.

Reproductive Allocation

The percentages of reproductive allocation in the species studied at the different sites are shown in Table (7.2). All species allocated more dry matter to vegetative reproduction than to sexual reproduction. The percentage of SRA ranged from 1.4% in *D. octopetala* to 14.6% in *S. caespitosa*, while VRA was as high as 48.5% in *S. bronchialis* and 91% in *S. acaulis*.

Table (7.2) Average percentages of vegetative reproductive allocation (VRA) and sexual reproductive allocation (SRA) of the studied species. Dead organic matter is not included in the original dry phytomass. Standard deviation in parentheses. Underlined numbers in same column/species showed non-significant differences from each other.

Species and Site	Original dry phytomass (g)	% SRA	% VRA	SRA/VRA ratio
Eriogonum androsaceum				
Upper crest	50(16)	05.4(2.2)	75.6(12.5)	0.07(0.03)
Ridge (SW)	89(14)	06.3(2.8)	80.8(10.2)	0.08(0.02)
Lower slope (SW)	52(13)	07.1(1.5)	72.0(10.8)	0.10(0.05)
Potentialla uniflora				
Upper crest	42(10)	05.6(2.7)	80.0(08.5)	0.07(0.02)
Ridge (SW)	65(08)	04.1(3.0)	83.4(07.2)	0.05(0.03)
Lower slope (SW)	64(12)	05.2(2.5)	81.4(10.5)	0.06(0.02)
Saxifraga caespitosa				
Ridge (SW)	07(02)	14.6(3.4)	69.6(12.7)	0.21(0.10)
Saxifraga bronchialis				
Ridge (SW)	11(04)	08.4(4.6)	48.5(15.3)	0.20(0.08)
North-east side	14(03)	08.2(4.5)	50.3(16.5)	0.20(0.10)
Silene acaulis				
Ridge (SW)	26(06)	04.2(2.4)	84.9(08.3)	0.05(0.02)
Upper crest	21(08)	02.6(1.2)	91.0(05.5)	0.03(0.01)
North-east side	37(06)	03.7(1.8)	82.0(07.6)	0.04(0.02)
Dryas octopetala				
Upper crest	44(15)	01.4(0.8)	86.5(10.2)	0.02(0.01)
North-east side	88(12)	03.6(1.5)	82.4(11.8)	0.04(0.01)

Comparisons of SRA of the different species reveal non-significant differences among sites except for *D. octopetala* which attained significant difference between crest and north-east site and *S. acaulis* between ridge and crest. Differences in VRA among sites of four species were non-significant, with the exception of *E. androsaceum* where VRA on the ridge was significantly different from the other two sites.

The ratios of SRA/VRA show that all studied species allocated more dry matter to vegetative reproduction than sexual reproduction. The ratios ranged from 0.02 in *D. octopetala* to 0.21 in *S. caespitosa* which showed the highest ratio among the six species. The ratios did not differ significantly between sites.

D. Discussion

The fact that all cushion plants on Mount Allan allocated more assimilates to vegetative than to sexual reproduction does not characterize them perfectly as pioneer species. According to Odum (1969) one would expect the opposite. On the other hand there is a difference in grade of allocation among the cushion plant species. *E. androsaceum* and *P. uniflora* growing over a wide range of the very unstable SW-slopes had SRA values from 4.1% to 7.1% of the total dry matter and VRA ranged from 72% to 83.4%. The values for *S. acaulis* and *D. octopetala*, both growing on the much more stable NE slope, differed remarkably. These two species allocated more matter toward vegetative reproduction, and SRA + VRA combined were higher here than for the SW-slope cushion plants. A number of interpretations of such events have been put forward. Abrahamson (1975) pointed out, that the allocation of more resources to vegetative organs may enhance the competitive ability of a plant, while Zeide (1978) and Jolls (1982) suggest that the transition from one reproductive strategy to another can be explained as a redistribution of resources accumulated in advance to enable the plants to be independent of environmental severity. Alternatively, the reduction of sexual reproduction in such an environment is considered to result from lack of special adaptations to the usually severe habitats (Bell and Bliss 1980).

From the data and observations on Mt. Allan one may conclude that differences in resource allocation among cushion plants reflect their different roles in colonizing such mountain sites. Succession on an unstable, steep slope proceeds very slowly and cannot be considered as classical succession sensu Clements (1916), Gams (1918) or Tansley (1935). The variety of stresses during the growth season (variable temperatures, strong winds, varying soil moisture conditions) is not selecting for therophytes or biennials. Hence high SRA is not to be expected as in other early successional plants. On steep, dry mountain slopes, where the surface layer of the ground consists of unpredictably moving rocks and gravel, vegetative reproduction can be considered as the more successful strategy. It does not, however, exclude reproduction by seeds, as demonstrated in Chapter V. So it is not surprising to find *E. androsaceum* and *P. uniflora* with their high VRA values and relatively better performance in SRA as compared to *S. acaulis* and *D. octopetala* as the main colonizers on those unstable slopes. *S. acaulis* and *D. octopetala* on the other hand live in more stable conditions, which may be considered to be approaching the climax state of the cushion plant community. Cover values are much higher, soil is better developed, and much less solifluction occurs. Higher VRA values in this area fit very well.

The higher values of VRA + SRA combined as compared on the more hostile SW slopes may be seen as the result of the better overall conditions on the NE-slope (more moisture, more developed soil, less stress).

The two *Saxifraga* species studied exhibit different altitudinal distribution and showed different resource allocation patterns. *S. caespitosa* which is restricted to the ridge site showed higher resource allocation to both sexual (14.6%) and vegetative reproduction (69.6%) than *S. bronchialis* which exists on both windward and lee slopes. The non-significant differences in resource allocation between sites shown by *S. bronchialis* may be due to the fact that the plant mostly exists in microsites between rock outcrops which are more or less similar on both windward and lee mountain sides. These reproductive allocation patterns are similar to those reported by Stewart (1984) and Grulke and Bliss (1985).

Besides genetically controlled differences in resource allocation between the various species, phenotypic adaptations may occur. Between site differences (plastic responses) can be interpreted as a strategy allowing habitation of a range of environmental conditions (Bradshaw 1965, Hickman 1975, Soule and Werner 1981, Grime et al. 1986), or as an expression of phenotypic plasticity and genetic differentiation (Abrahamson 1975, Roos and Quinn 1977, Soule and Werner 1981). Others suggest that plastic responses in resource allocation can be explained in terms of the levels of competition at each site (Werner 1976, Stewart and Thompson 1982), or may be due to macro- and microenvironmental factors (Pitelka 1977, Jaksic and Montenegro 1979, Whittaker and Goodman 1979). Hickman (1975) observed that mountain plants in open habitats showed a highly plastic response in reproductive allocation patterns in different habitats.

In addition, the following particular mechanisms may contribute to the propagation of cushion plants on the SW slope, thus reducing the selective pressure for more reproduction. The continual downward movement of sliding snow and rock fragments in unstable sites, may uproot the whole plant, or pull apart most of the vegetative organs. These detached propagules are carried away into other areas. The same role is played by digging and burrowing animals which tear the plants into propagules due to their activities. Also, wind is an important factor in determining the pattern of transportation and distribution of such propagules. Wind exposes the protected vegetative buds and growing apices by blowing some of the packing material away. Drifting material may later be stranded among rocks in sheltered crevices, and give rise to further individuals. Since transported plant propagules often are loaded with substantial amounts of organic matter, development may be enhanced. As long as sliding rock fragments do not bring about its destruction, the newly established propagules continue to form new individuals.

Generally, the instability of substratum is disadvantageous to the process of colonization of pioneer plants. For cushion plants it is sometimes also an advantage to their vegetative reproduction as demonstrated in Chapter IV.

Each of the six species studied is adapted to a particular set of environmental conditions and able to perpetuate itself within a limited range of conditions. Differences in resource allocation appear to be adaptive responses to site conditions.

E. Summary

1. The comparison of sexual and vegetative reproductive allocation in terms of dry matter showed higher allocation to vegetative than to sexual reproduction at

all sites (altitudes). The least emphasis on sexual reproduction was at the highest altitude (crest).

2. Along an altitudinal range of environmental conditions, differences in resource allocation within a particular species appear to be adaptive responses to site conditions.
3. Species which have a narrow range of distribution (e.g *Saxifraga caespitosa*) allocate more resources to reproduction than species with a wide range.
4. Species with similar ranges of distribution showed similar resource allocation to reproduction. For those on the SW side (*Eriogonum androsaceum* and *Potentilla uniflora*) sexual reproduction is more important than for those on the NE side (*Silene acaulis* and *Dryas octopetala*).
5. Differences in resource allocation allow, among other characteristics, the separation of some cushion plants on Mt. Allan to at least, two groups: a) typical pioneers (*Eriogonum androsaceum, Potentilla uniflora*) b) climax species (e.g. *Dryas octopetala*).
6. Some local factors such as wind, solifluction and animal activities play a significant role in vegetative reproduction and distribution of alpine cushion plants.

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VIII. Water Relations and Leaf Anatomy

A. Introduction

Adaptations affecting plant water economy must play a central role in survival and reproduction under extreme conditions. Such adaptations are frequently inferred from comparative morphological and anatomical studies. Since physiological adaptations are as important as morphologically and anatomically discernible ones, emphasis is given to all three of them in this chapter.

Although a number of ecophysiological studies on alpine plants have been conducted (as reviewed by Bliss 1962, Billings and Mooney 1968, Billings 1974a, Larcher 1980b, Bliss 1985), it is still difficult to conclude to what extent alpine plants share common physiological and anatomical features, and how different they are from "lowland" plants in this respect (Koerner et al. 1983). Studies of water relations of alpine/arctic plants (Bliss 1960, Spomer and Salisbury 1968, Anderson and McNaughton 1973, Ehleringer and Miller 1975b, Smith and Geller 1979, Chapin and Shaver 1985) suggest that differences in water regime among species exert some control over their local distribution. Their suggestions were based on observed differences in water relations between plants of wet and dry sites. Generally, species from wet sites transpire at higher rates than plants from dry sites.

There are some data available on water relations of cushion-plants (Heilborn 1925, Pisek et al. 1935, Berger-Landefeldt 1936, Hedberg 1964, Spomer 1964, Sveshinikova 1973, Courtin and Mayo 1975, Addison 1977, Izmailova 1977, Koerner and DeMoraes 1979, Oberbauer and Billings 1981). These authors have shown that cushion plants had more or less uniform water relations with high rates of transpiration. Wide variations in water content and water potential were indicative of frequent water stress in these plants. Transpiration, water content, water saturation deficit, and water potential are common indices which reflect the ability of plants to cope with prevailing environments (Larcher 1980a, and Kramer 1983). However, they do not suggest how the water balances of different plants growing together come to be different (Jarvis 1967).

Large portions of alpine areas have an abundance of water but the exposed sites inhabited by cushion-plants (screes, fellfields, ridges and rocky slopes) are known for frequent soil moisture stress. Alpine environments thus exhibit a large degree of microsite variability with respect to moisture. Some studies suggest that within the alpine zone of a mountain range, local distribution of plant species is largely determined by moisture and temperature gradients from windward slopes to lee slopes (Daubenmire 1943, Mooney et al. 1965, Billings and Mooney 1968, Johnson and Caldwell 1976, Oberbauer and Billings 1981). Soil moisture and temperature, therefore, may have a great effect on the water relations of cushion plants. The question then arises as to what extent the local distribution of alpine cushion plants can be linked with their water regime characteristics? The six species under investigation display a range of distribution in the alpine zone and it can be expected that a wide array of moisture conditions exists for the different species. Consequently, cushion plants have likely evolved different physiological adaptations corresponding to their distribution.

Some researcher such as Oppenheimer (1960), Small (1973), Bocher (1979), Peace and Macdonald (1981) have suggested that the xeromorphic features in plants other than desert plants can be attributed to 1) periodic water stress, 2) soil mineral deficiency and 3) low primary productivity. For alpine cushion plants, these three factors may play a role in shaping their xeromorphic characteristics. The structural features of cushion plants, particularly those of leaves are of paramount importance, especially anatomical peculiarities related to gas exchange and water relations that lead to reduction of the transpiration rate and avoidance of desiccation. According to Larcher (1980a), the causes of specific differences in the net photosynthetic capacity are found in the effectiveness of the enzymes and the amount of photorespiration, as well as in anatomical peculiarities of leaf structure, the ease with which air passes through the intercellular system, and the shape and distribution of the stomata. Therefore an attempt will be made to correlate some anatomical characteristics of the leaves with the water relations of the plants. The objectives of this study were to: 1) determine in a comparative manner some characteristics of the water regime in cushion plants, 2) find out if water relation characteristics are important factors in determining the local distribution of alpine cushion plants and 3) compare and quantify the leaf anatomical features in the different species.

B. Materials and Methods

During the summer of 1983, samples of twenty to thirty mature individuals of six species (*Eriogonum androsaceum* Benth., *Potentilla uniflora* Ledeb., *Saxifraga caespitosa* L., *Saxifraga bronchialis* L., *Silene acaulis* L., and *Dryas octopetala* L.) were chosen which had an uniform size (about 10 cm surface diameter). They were transplanted into pots with soils consisting of one part peat and one part original soil from the alpine habitat on Mt. Allan (elevation of 2250 m above sea level). Plants were grown in controlled growth chambers at the University of Alberta Phytotron (14hr photoperiod at 20°C day and 10°C night). Light was provided by white fluorescent tubes supplemented by 20% incandescent bulbs. The total irradiance at the surface of plants was about 600 μmol.m^{-2}.sec^{-1}. Relative humidity ranged from 50 to 60% and wind velocity was about 0.5km h^{-1}. In order for acclimation and regeneration of roots, the plants were maintained in the growth chamber two months prior to the experiments. The samples were subwatered at weekly intervals.

For the study of the shoot water content. transpiration, water saturation deficit and water potential, four to five individual plants per species per group were separated into two groups. One week prior to measurement, in each species, one group of the plants was watered regularly, while the other group was subjected to water stress by withholding water for two more days. At the time of measurement, the soil moisture content of watered plants was about 20%, while for unwatered plants it was only 3% based on soil fresh weight. The plants were exposed to the test temperature (from 5 to 30°C) for 3 h before measurement. The methods of study were according to Slavik (1974). Four replicate samples(*E. androsaceum* and *S. caespitosa*) or five samples (*P. uniflora*, *S. bronchialis*, *S. acaulis* and *D. octopetala*) were used in every measurement.

The drying-out curves and water loss from cut-shoots were carried out on watered plants only.

Water Content

Water content (WC) of the vegetative rosettes was determined. Fresh weight and oven dry weight after drying for 48h at 70°C, allowed calculation of water content (% fresh weight) by the following formula:

WC = [(Fresh Weight - Dry weight)/Fresh Weight] x 100%

Transpiration

Water loss from detached green, leafy rosettes was measured over a 3 minute period by the "rapid weighing" torsion balance method. For comparative studies of different cushion plants, this method is the most convenient. The cut surface of detached parts was smeared with petroleum jelly and rapidly weighed, then the plant was exposed to the conditions of the growth chamber for 3 min and weighed again. The decrease in weight corresponds to the water lost by transpiration during the period of exposure. Transpiration rates are expressed in mg/g/h based on fresh weight.

Water Saturation Deficit

Water saturation deficit is the amount of water which the plant requires to reach full saturation. After its fresh weight determination, leaf rosettes were placed in a large, covered petri dish which was filled with water. The stems and leaves were immersed in water and were kept in the dark at room temperature for 24 h. The 24 h period was found to be sufficient to saturate the individual leaves of the rosettes. Saturated weight and oven dry weight were determined. The water saturation deficit (WSD) was calculated by the following formula

$$\text{WSD} = [(\text{Saturated Weight} - \text{Initial Fresh Weight}) / (\text{Saturated Weight} - \text{Dry Weight})] \times 100\%$$

Water Potential

Xylem pressure potentials of shoots were measured using a Scholander pressure chamber (PMS Instruments Co.). The pressure measured in this way compensates the original negative pressure in the xylem vessels (Scholander et al. 1965). A leafy shoot was detached as quickly as possible and enclosed in the steel pressure chamber so that the cut end of the stem protruded (about 2 cm) from the chamber. The pressure inside the chamber was gradually increased (about 0.7 bar sec^{-1}) by adding compressed nitrogen until small sap droplets appeared on the cut surface. A hand lens or binocular microscope was used to view the sap droplets.

Drying-out Curves

This experiment was designed to test the ability of the plants to restrict water loss. It was based on a technique used by Buckley et al. (1980) following Pisek and Winkler (1953). After fresh weight determination, leaf rosettes were placed in covered petri dishes filled with water for 24h at room temperature until fully saturated. They were then dried superficially with blotting paper and saturated weight was determined. The materials were left on a tray in diffuse natural light and weighed on an electronic balance at intervals of 10 min for the first 90 min, and at intervals of 30 min thereafter. After 5 hours the materials were oven dried for 48 h at 70°C and dry weights were determined. Plots of fresh weight against time were used to determine whether phases in drying-out of the shoot correspond to a period with stomata open and a period with them closed.

The saturated water content, water deficit at apparent start and end of stomatal closure, and rate of water loss after one hour following apparent stomatal closure were determined for the different species. Water loss after stomatal closure was considered as the cuticular transpiration.

Water Loss from Cut Shoots

To determine water loss from cut shoots in a 24 h period, transpiring shoots were weighed immediately after cutting. They were brought to saturation, then were left to dry at room temperature beside a window. There was diffused natural light by day and relatively dim artificial lighting in the evening. Atmospheric conditions were approximately constant. The shoots were weighed after 24 h and oven dry weights were determined. Percentages of loss of water content per saturated water content, and the percentage of loss of fresh weight per saturated fresh weight were determined.

A copper constantan thermocouple was used to measure leaf temperature.

Anatomical Investigations

Leaves from every species were collected in the field and fixed in formalin-acetic acid-alcohol (FAA) mixture

(90:5:5). They were transfered later to 50% ethanol and then were processed in the lab for anatomical studies. All leaves used in the investigation appeared mature and healthy and were collected from similar orders on each rosette.

For anatomical measurements, the preserved materials were dehydrated in an ethyl-tertiary-butyl-alcohol series, infiltrated, and then were embedded in paraffin using a standard procedure (O'Brien and McCully, 1981). Sections were cut on a microtome at a thickness of 15 μm in a plane perpendicular to the midrib. Tissue sections were stained in safranin and fast green. Measurements were recorded from 10 cross sections (from five leaves per species) in each case using an ocular micrometer. The area of xylem elements was expressed with reference to the mass of the plant parts supplied as a relative conducting area ($mm^2.g^{-1}$). Leaf volume (V) was calculated from the equation V = SLA X thickness of lamina (mm), where SLA is the specific leaf area and is obtained as following: SLA = (surface area of the leaf)/(fresh weight) = $mm^2.mg^{-1}$.

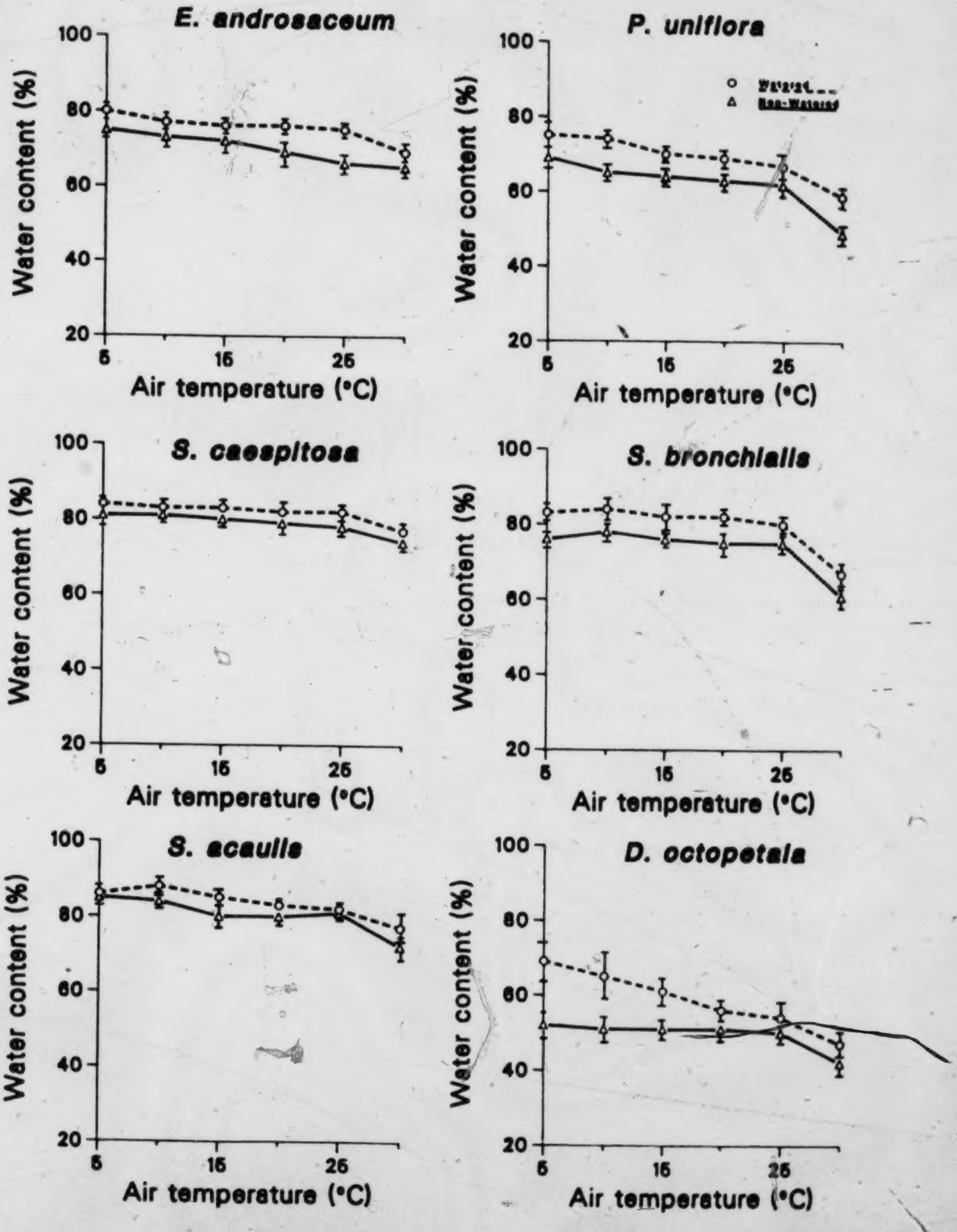
Stomatal density is expressed as the number of stomata per square millimeter. Stomatal index (SI) was calculated by applying the formula: SI = [S/(E+S)] X 100%, where S is the number of stomata per unit area and E is the number of epidermal cells in the same area. Removal of the epidermis for stomatal studies was accomplished by incubation of 2 mm pieces from fresh leaves in a macerating fluid glacial acetic acid-hydrogen peroxide and distilled water (40:40:20) at 45°C for about 20 to 40 hours depending on leaf type following a technique modified by Boulous and Beakbane (1971). The epidermis was peeled off and examined under the light microscope. Stomatal measurements were made on 5 leaves of each species and in 10 randomly chosen microscopic fields (area 0.16mm² excluding major veins) of each leaf peeling. Each figure in the text is thus a mean based on 50 microscopic fields.

C. Results

Water Content

In all species investigated, the percentage of water content was highest at low temperatures and decreased with a rise in temperature (Fig.8.1). For both watered (W) and non-watered (NW) plants, *Silene acaulis* has the highest average water content of 84 (W)/80 (NW)%, which fluctuated within a range of 77-85% (W) and 72-80% (NW). In contrast, *Dryas octopetala* exhibited the lowest average water content of 59 (W)/50 (NW)%, for which fluctuation ranges of 47-69% (W) and 42-52 (NW) were attained. The remaining species had intermediate values. A one-way ANOVA was done to determine

Figure (8.1): Water content (% fresh weight) of transpiring organs at different air temperatures (°C) and water treatments (watered/nonwatered). Vertical bars indicate the standard deviations. t-Test showed significant differences between watered and nonwatered groups at the 95% level (o-----o watered; Δ———Δ non-watered).


E. androsaceum
P. uniflora
Watered
Non-Watered
S. caespitosa
S. bronchialis
S. acaulis
D. octopetala
Water content (%)
Air temperature (°C)
100
80
60
40
20
5
15
25

if there were significant differences among the mean values (95% probability level). If the average water content over the tested temperature range is taken as a measure, the following sequence (from highest to lowest values) of the species was observed for W plants: *S. acaulis* ≃ *S. caespitosa* ≃ *S. bronchialis* > *E. androsaceum* ≃ *P. uniflora* > *D. octopetala.* The sequence changed for NW plants: *S. acaulis* ≃ *S. caespitosa* > *S. bronchialis* > *E. androsaceum* > *P. uniflora* > *D. octopetala.*

The watering of plants increased water content to different degrees depending on species and temperature treatment. The influence of watering was least at high temperatures. Judging from the overall averages, watering increases the water content but not as much as transpiration rates particularly at high temperatures (App.14). By using the ratio of average values attained for W to those for NW plants to evaluate the plant respose to watering, the following sequence was obtained from highest value to lowest: *D. octopetala* ≃ *P. uniflora* > *E. androsaceum* ≃ *S. bronchialis* > *S. caespitosa* ≃ *S. acaulis.* This indicates that the first two species are able to alter their water content over a wide range according to conditions. In *S. caespitosa* and *S. acaulis*, responses to watering were the least while *E. androsaceum* and *S. bronchialis* showed an intermediate response.

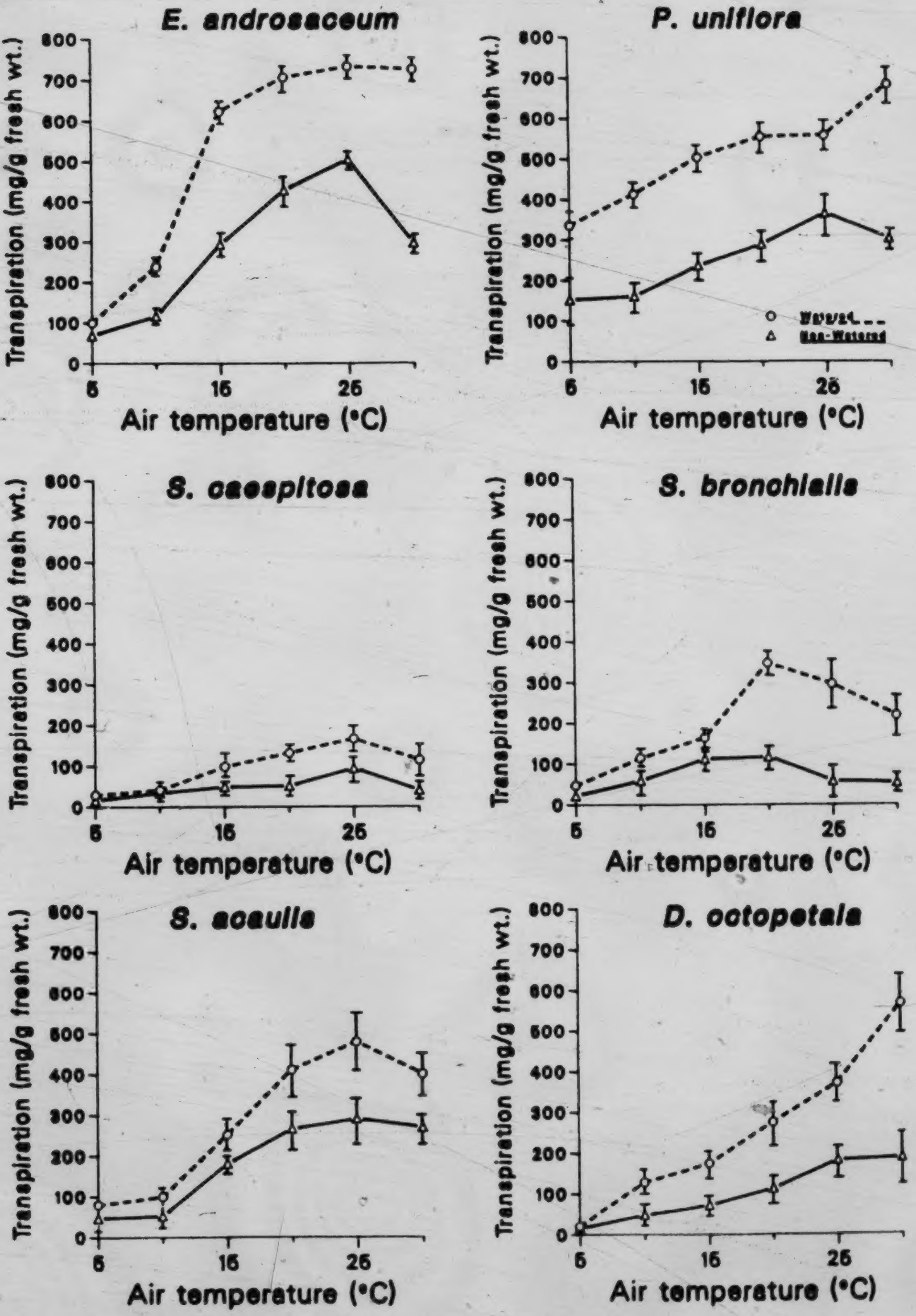
Transpiration

Most of the species tested were found to have relatively high transpiration rates even under dry soil conditions. As far as interspecific differences are concerned, *E. androsaceum* had by far the highest average transpiration rate of all species investigated (Fig.8.2). It attained values of 520 and 284 mg/g/h for both W and NW plants, respectively. Meanwhile, *S. caespitosa* exhibited the lowest rate of transpiration with average values of 97 and 47 mg/g/h for W and NW plants. Intermediate rates were shown by the four remaining species. If the average transpiration rate is taken as a measure, the following sequence of species (from highest to lowest values) was observed for both W and NW plants: *E. androsaceum* > *P. uniflora* > *S. acaulis* > *D. octopetala* > *S. bronchialis* > *S. caespitosa*.

In all species, watering increased the transpiration rate, however to different degrees depending on species and temperature treatment. The influence of watering is least at low temperatures. By using the ratio of average values attained for watered to those for non-watered plants to evaluate the plant response to watering, transpiration showed higher response to watering than water content of the plants (App.14). The ratios ranged from 1.56 in *S. acaulis* to 2.54 in *S. bronchialis*.

0

Figure (8.2): Transpiration rates (mg/g fresh weight/hour) at different air temperatures (°C) and water treatments (watered/nonwatered). t-Test showed significant differences over the tested temperature range at the 95 % level.


E. androsaceum
P. uniflora
S. caespitosa
S. bronchialis
S. acaulis
D. octopetala
Transpiration (mg/g fresh wt.)
Air temperature (°C)
0
100
200
300
400
500
600
700
800
5
15
25
○ Watered - - -
△ Non-Watered

When these ratios are considered, the following sequence (from highest to lowest values) appeared: *S. bronchialis* ≃ *D. octopetala* > *S. caespitosa* ≃ *P. uniflora* > *E. androsaceum* ≃ *S. acaulis*. This indicates that species with higher transpiration rates responded least to watering.

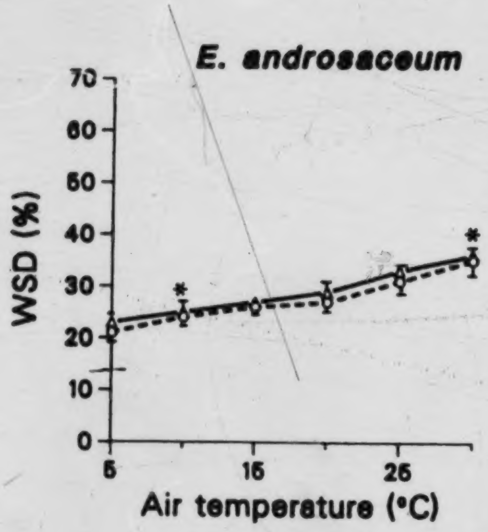
Water Saturation Deficit

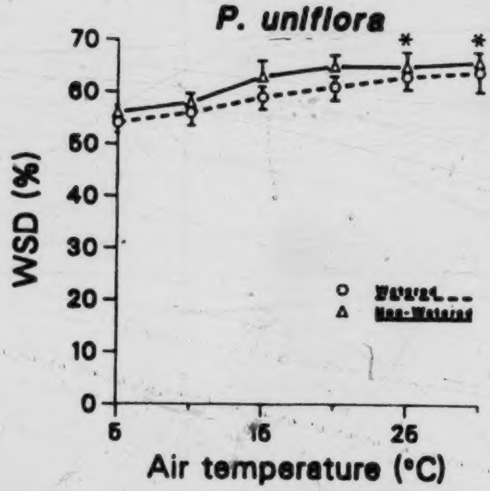
The values of WSD show wide variation among the species. Watered plants of course have lower WSD. WSD's were lowest at low temperatures and increased with increasing temperature (Fig 8.3). This refers to the depletion of the water content due to increased transpiration. For both W and NW plants, *P. uniflora* has the highest average WSD at all temperature treatments of 60 (W)/62 (NW)%, which fluctuated within a range of 54-64% (W) and 56-66% (NW). *S. acaulis* exhibits the lowest mean of WSD (17% W/19% NW), with fluctuation ranges of 14-22%(W) and 16-23%(NW). The remaining species had intermediate values.

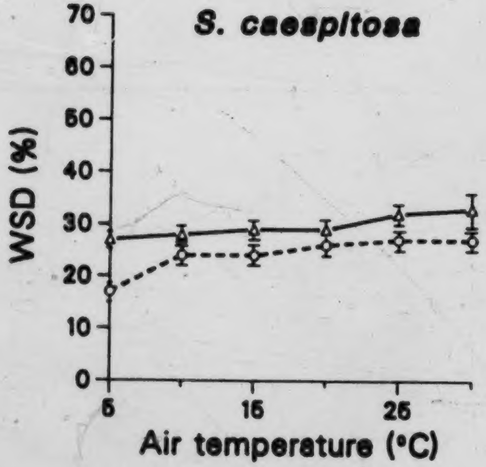
If average WSD is taken as a measure, the following sequence (from highest to lowest) of the species was observed for W and NW plants: *P. uniflora* > *D. octopetala* > *E. androsaceum* ≃ *S. caespitosa* > *S. bronchialis* ≃ *S. acaulis*. The high WSD values appeared to exercise restraining effects on water loss.

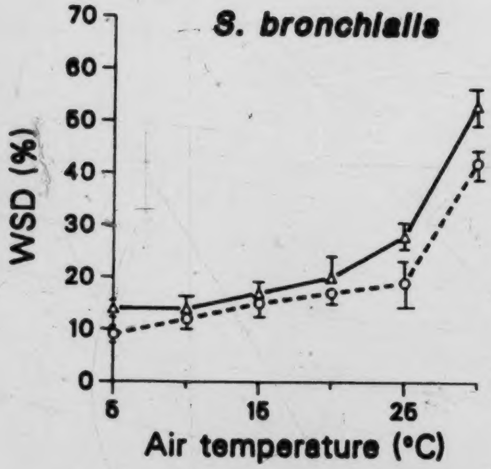
0

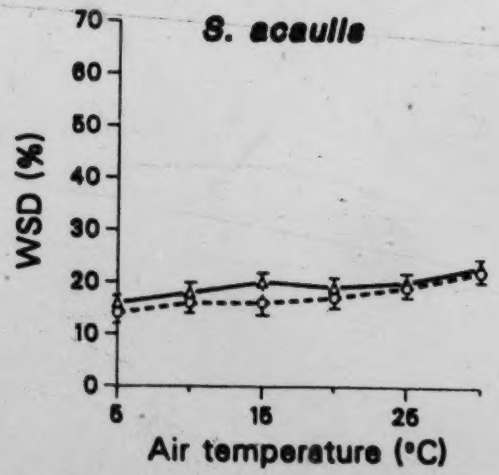
Figure (8.3): Water saturation deficits (%) of the transpiring organs at different air temperatures (°C) and water treatments (watered/nonwatered). * indicates non-significant differences.

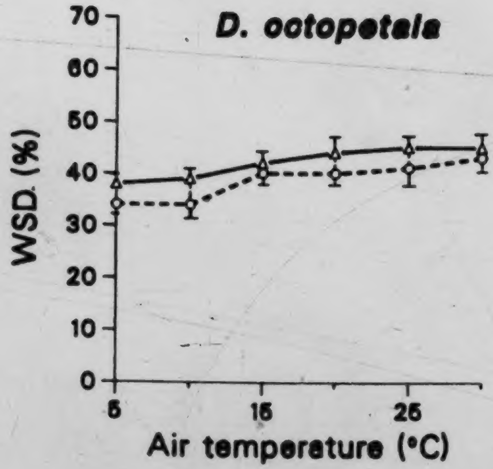

E. androsaceum
WSD (%)
70
60
50
40
30
20
10
0
5
15
25
Air temperature (°C)
*
*


P. uniflora
WSD (%)
70
60
50
40
30
20
10
0
5
15
25
Air temperature (°C)
*
*
○ Watered
Δ Non-Watered


S. caespitosa
WSD (%)
70
60
50
40
30
20
10
0
5
15
25
Air temperature (°C)


S. bronchialis
WSD (%)
70
60
50
40
30
20
10
0
5
15
25
Air temperature (°C)


S. acaulis
WSD (%)
70
60
50
40
30
20
10
0
5
15
25
Air temperature (°C)


D. octopetala
WSD (%)
70
60
50
40
30
20
10
0
5
15
25
Air temperature (°C)

In most species, when WSD rose above 30%, the rate of transpiration was reduced. Distinguished from other species, *S. broncialis*, shows a sudden rise in WSD at 30°C.

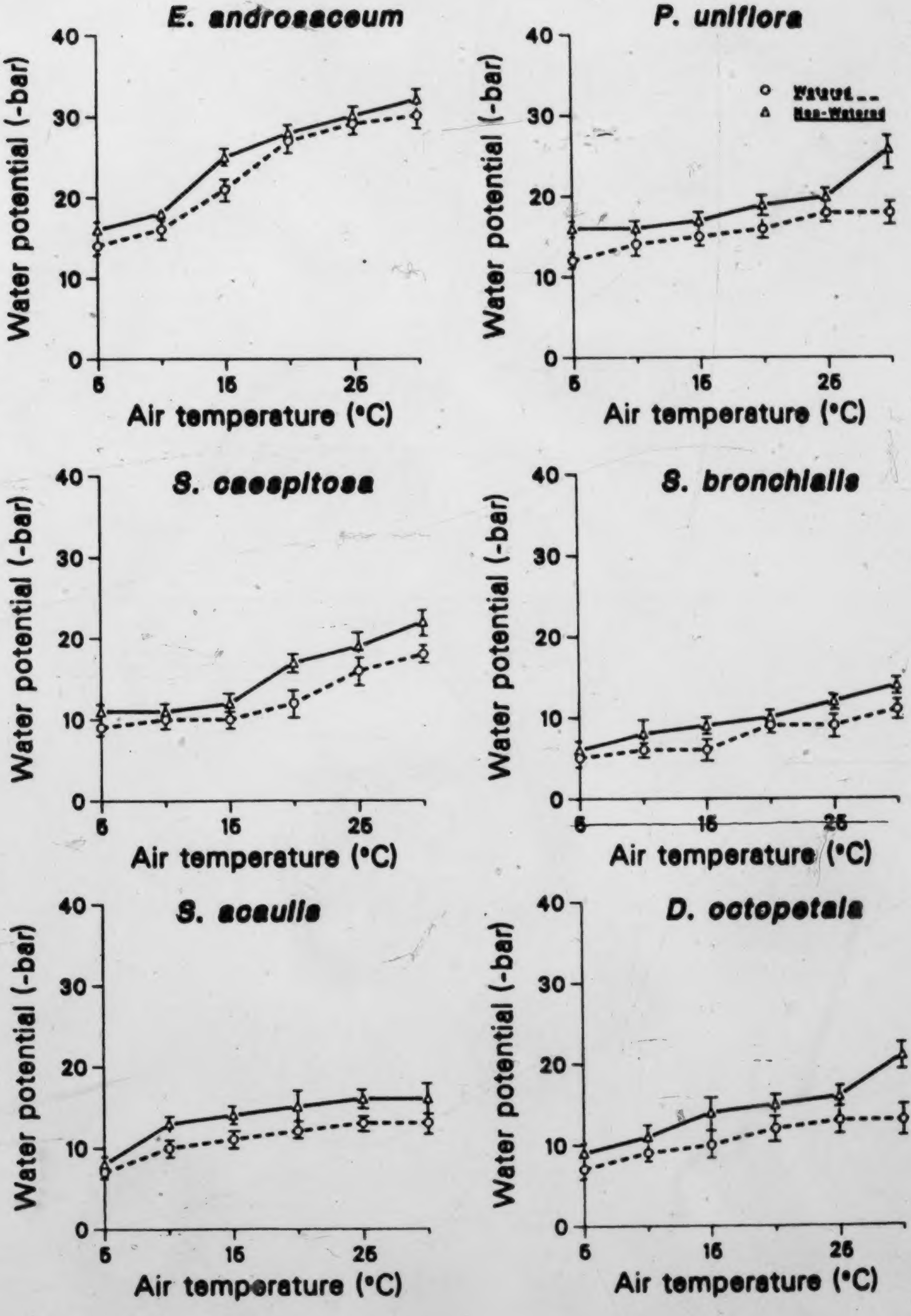
The ratio of the average WSD values obtained from NW to those for W plants is used to estimate the influence of watering on WSD of different species. The species with higher WSD responded least to watering. This can be attributed to the high transpiration rates of the former. Watering caused WSD to decrease by factors of 1.26, 1.25 and 1.12 in non-watered *S. bronchialis*, *S. caespitosa*, and *S. acaulis*, respectively (App.14). In *D. octopetala*, this factor was 1.08, whereas in *E. androsaceum* and *P. uniflora*, the factors were 1.04 and 1.03 respectively. By using the average WSD ratio of NW to W plants, the following sequence (from highest to lowest) of the species was obtained: *S. bronchialis* ≃ *S. caespitosa* > *S. acaulis* ≃ *D. octopetala* > *E. androsaceum* ≃ *P. uniflora*.

Water Potential

All of the species tested showed decreased water potential (more negative) when temperature rose. (Fig.8.4) This was true for both watered and non-watered plants. The water potentials measured on various species covered a wide range and they correlated with plant water content and water deficit.

0

Figure (8.4): Water potentials (-bar) of the transpiring organs at different temperatures (°C) and water treatments (watered/nonwatered). t-Test showed significant differences over the tested temperature range at the 95% probability level.


E. androsaceum
P. uniflora
S. caespitosa
S. bronchialis
S. acaulis
D. octopetala
○ Watered - -
△ Non-Watered —
Water potential (-bar)
0
10
20
30
40
Air temperature (°C)
5
15
25

At one extreme, *S. bronchialis* had the highest average potential (least negative) of -10(NW) and -8(W) bar with a range of -6 to -14 (NW)/-5 to -11(W) bar. At the other extreme, *E. androsaceum* had the lowest average water potential (most negative) at -25 (NW) and -23 (W) bar, with a range of -16 to -32 bar and -14 to -30 bar for NW and W plants respectively. The remaining species have exhibited intermediate values. I~~f~~ average water potential is taken as a measure, the following sequence from the highest (least negative) to the lowest (most negative) of the species was observed for both W and NW plants: *S. bronchialis* > *S. acaulis* ≃ *D. octopetala* ≃ *S. caespitosa* > *P. uniflora* > *E. androsaceum*.

The influence of watering on water potential can be estimated by calculating the ratio of average values obtained for NW to those for W plants (App.14). Species with high water potential such as *Saxifraga bronchialis* and *Silene acaulis* responded most to watering. On the average, watering caused the water potential to rise by a ratio of 1.25 and 1.27 compared to NW *S. bronchialis* and *S. acaulis* plants, respectively. On the other hand for *Eriogonum androsaceum* with the lowest water potential, this ratio was 1.1, whereas in *Potentilla uniflora* and *Saxifraga caespitosa*, watering had an intermediate effect on their water potential. By using the average water potential ratio of NW to W plants, the following sequence (from highest to lowest) of the species can be obtained: *S. acaulis* ≃ *D.*

octopetala ≃ *S. bronchialis* > *P. uniflora* ≃ *S. caespitosa* ≃ *E. androsaceum*. This indicates that species with the lowest water potential responded least to watering.

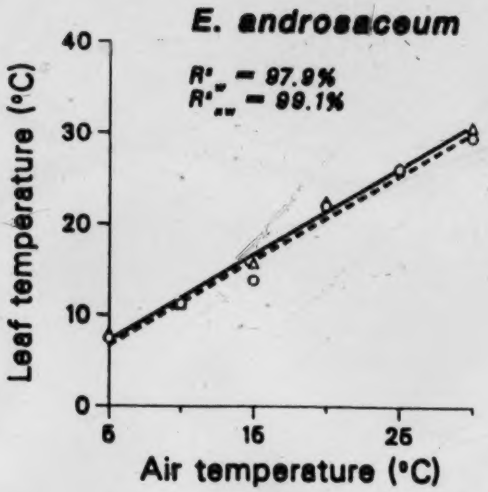
Leaf Temperature

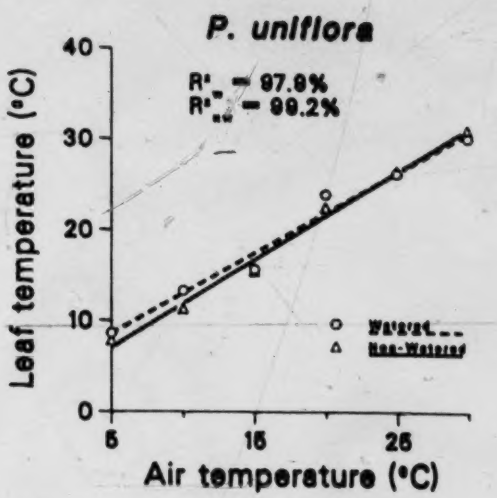
Plants of all species had higher leaf temperatures than air temperature with the exception of *E. androsaceum* (watered) which showed lower leaf temperature than the air at temperatures of 15 and 30°C (App.15). In most species at low air temperatures, the leaf temperatures of NW plants were lower than or equal to leaf temperatures of W plants. The opposite was true at higher air temperatures. At intermediate temperatures (around 15°C), there was little difference between leaf temperatures of W and NW plants (Appendix 15). Superimposed curves are shown in Fig.(8.5). The t-Test for the regression lines of five species for both watered and non-watered plants did not show significant differences (95 % level) in slope and interception. Only *Dryas octopetala* showed significant differences.

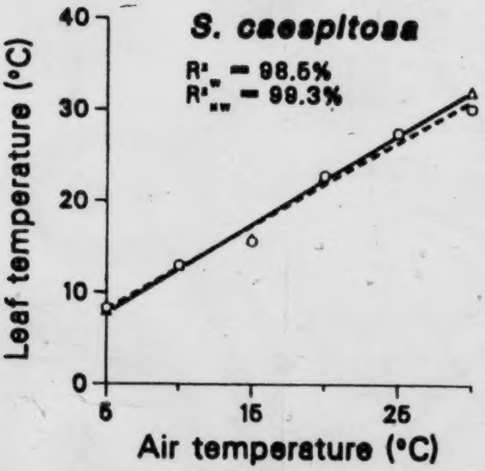
Measurements were taken in a growth chamber at an air velocity of 0.5 km h^{-1}; this increases the thermal conductivity of the leaves. Accordingly, excess leaf temperatures may be reduced to a great extent.

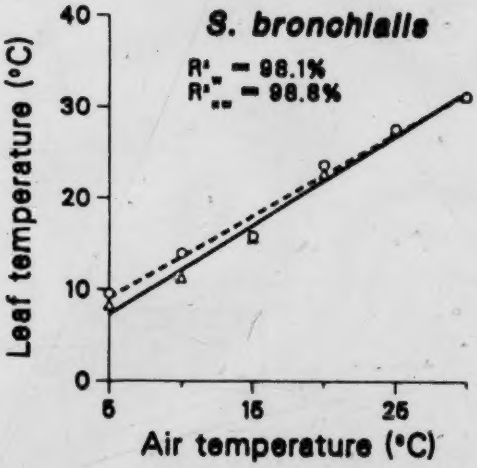
0

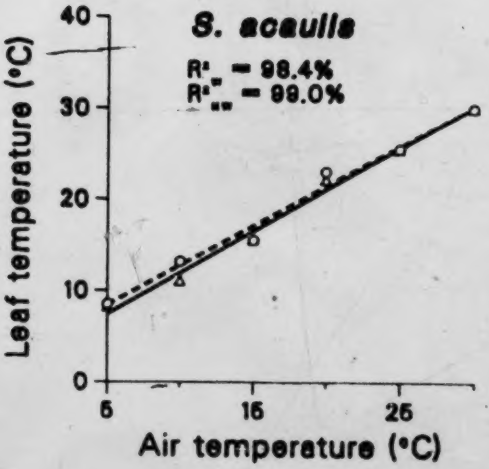
Figure (8.5): Linear regression of leaf temperatures over air temperatures (°C) at different water treatments (watered/nonwatered).

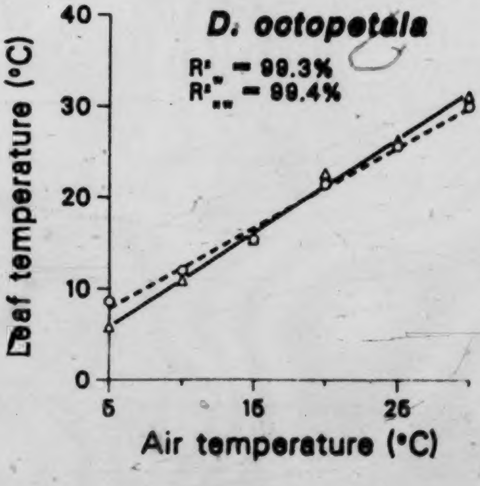

E. androsaceum
R²w = 97.9%
R²nw = 99.1%
Leaf temperature (°C)
0
10
20
30
40
Air temperature (°C)
5
15
25


P. uniflora
R²w = 97.9%
R²nw = 99.2%
Watered
Non-Watered
Leaf temperature (°C)
0
10
20
30
40
Air temperature (°C)
5
15
25


S. caespitosa
R²w = 98.5%
R²nw = 99.3%
Leaf temperature (°C)
0
10
20
30
40
Air temperature (°C)
5
15
25


S. bronchialis
R²w = 98.1%
R²nw = 98.8%
Leaf temperature (°C)
0
10
20
30
40
Air temperature (°C)
5
15
25


S. acaulis
R²w = 98.4%
R²nw = 99.0%
Leaf temperature (°C)
0
10
20
30
40
Air temperature (°C)
5
15
25

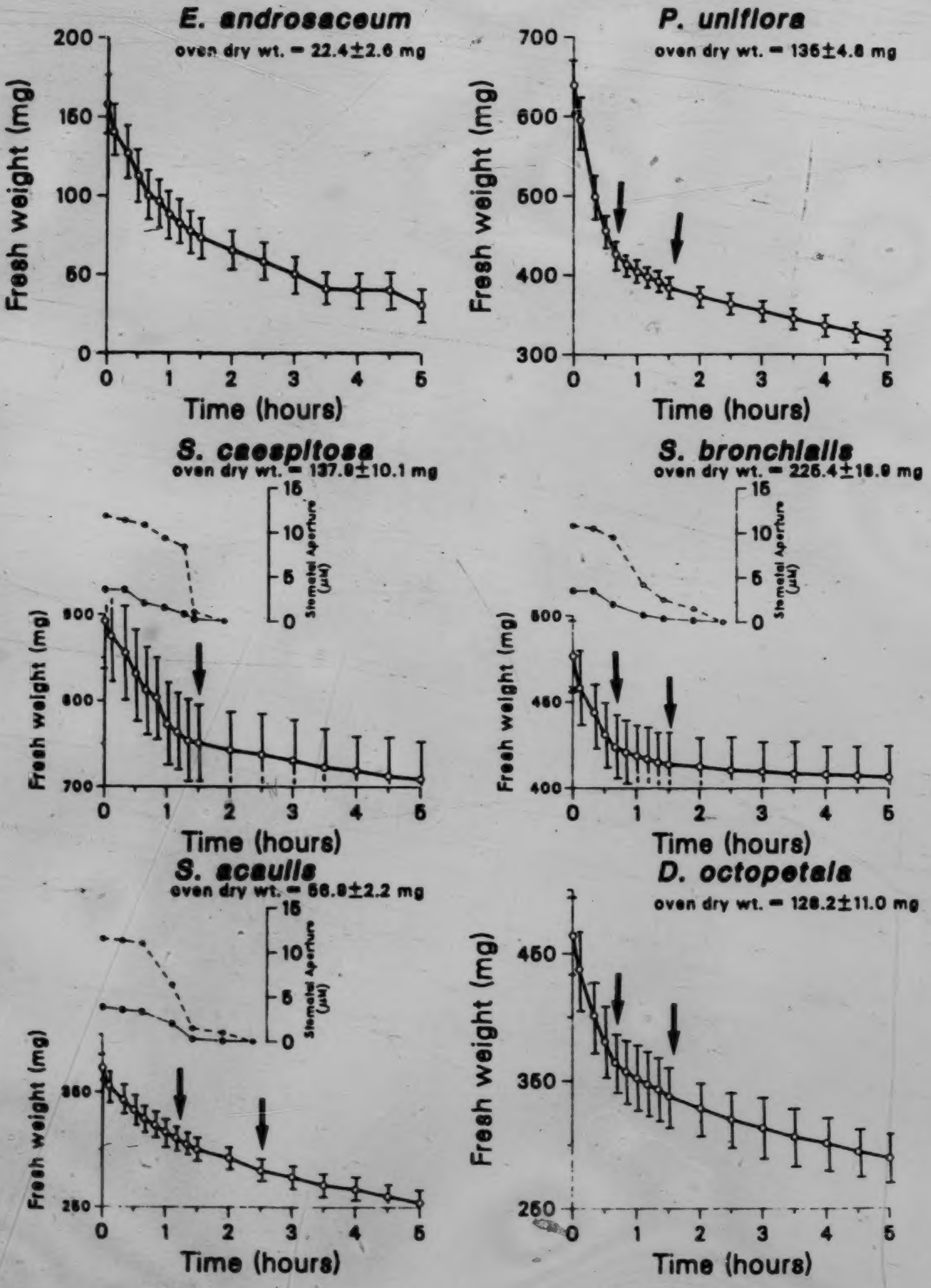

D. octopetala
R²w = 99.3%
R²nw = 99.4%
Leaf temperature (°C)
0
10
20
30
40
Air temperature (°C)
5
15
25

Meanwhile, it may be assumed that because the leaves of W plants transpire more than those of NW plants, the lower temperatures of W plants can be attributed to the cooling effect of transpiration. However, transpiration did not cool the leaves below air temperatures.

Drying-out Curves

The drying-out curves of the species examined are shown in Figure(8.6). Three types of curves were distingushed; 1) curves with a single sharp inflexion, e.g. *Saxifraga caespitosa*. 2) Curves with two inflexions as appeared in *Saxifraga bronchialis, Silene acaulis, Potentilla uniflora*,and *Dryas octopetala*. 3) Curves with no prominent inflexion, e.g. *Eriogonum androsaceum*. However, this graph indicates erratic stomatal movement. In the first type, the single inflexion is conventionally interpreted as the point at which apparent simultaneous closure of stomata occurs. The initial steady decline represents water loss through stomata and the cuticle and the second phase of the curve represents water loss through the cuticle alone.

Figure (8.6): Drying-out curves and stomatal aperture (o-----o length, and •——• width) of detached transpiring shoots. Arrows indicate the apparent inflexion points. The inflexion points are eye-fitted based on stomatal apperture and loss of fresh weight over time. Vertical bars indicate standard deviation.


E. androsaceum
oven dry wt. = 22.4±2.6 mg
Fresh weight (mg)
200
150
100
50
0
0 1 2 3 4 5
Time (hours)
P. uniflora
oven dry wt. = 136±4.8 mg
Fresh weight (mg)
700
600
500
400
300
0 1 2 3 4 5
Time (hours)
S. caespitosa
oven dry wt. = 137.9±10.1 mg
15
10
5
0
Stomatal Aperture (µM)
900
800
700
Fresh weight (mg)
0 1 2 3 4 5
Time (hours)
S. bronchialis
oven dry wt. = 225.4±18.9 mg
15
10
5
0
Stomatal Aperture (µM)
500
450
400
Fresh weight (mg)
0 1 2 3 4 5
Time (hours)
S. acaulis
oven dry wt. = 56.9±2.2 mg
15
10
5
0
Stomatal Aperture (µM)
350
250
Fresh weight (mg)
0 1 2 3 4 5
Time (hours)
D. octopetala
oven dry wt. = 128.2±11.0 mg
Fresh weight (mg)
450
350
250
0 1 2 3 4 5
Time (hours)

In the second type of curve, three phases are seen, suggesting that stomatal closure proceeds in two distinct episodes; the first inflexion represents partial closure of stomata (stimulated to shut), while the second inflexion represents complete stomatal closure (Appendix 16). Both inflexions occured at widely different water deficits.

The WSD at the end of stomatal closure (second inflexion) was more than two times and as much as four times the WSD at start of stomatal closure (first inflexion), with the exception of *S. acaulis* which showed the least variation (Table 8.1). The widely distributed species in the study area such as *E. androsaceum*, *P. uniflora* and *D. octopetala* tend to close their stomata at greater water deficits than narrowly distributed species. The mechanism is of great importance for gas exchange. The rates of water loss after apparent stomatal closure are presented in Table(8.1). The rates were found to fall between 1.6 mg/g/h in *S. bronchialis* to 8.6 mg/g/h in *S. acaulis*.

Stomatal aperture (width and length) was measured directly by pulling off the lower leaf epidermis. Epidermal strips were mounted in absolute ethyl alcohol and examined. Rarely was it found that on one leaf some stomata were open and others were closed.

Table (8.1): Percentage water contents at saturation, water content at the beginning and completion of stomatal closure, and rates of water loss with stomata closed. Standard deviation in brackets.

Species	Saturated water content (%)	water deficit % at		rate of water loss after stomatal closure	n
		start of stomatal closure	end of stomatal closure		
Eriogonum androsaceum	85.8(1.1)	4.8(0.8)	12.5(1.6)	8.3(1.5)	4
Potentialla uniflora	78.9(1.2)	3.7(0.9)	12.7(0.5)	3.4(0.3)	5
Saxifraga caespitosa	84.6(1.5)	———	07.6(0.4)	5.2(0.5)	4
Saxifraga bronchialis	85.9(0.9)	3.4(0.6)	06.5(0.3)	1.6(0.8)	5
Silene acaulis	87.7(1.6)	7.3(0.7)	09.1(0.4)	8.6(1.2)	5
Dryas octopetala	72.3(1.5)	3.8(0.5)	16.9(1.1)	3.7(0.4)	5

The values of stomatal aperture measurements are plotted on the drying-out curves of *S. caespitosa*, *S. bronchialis* and *S. acaulis* (Figure 8.6). Length always exceeded the width. The stomata were more open (greater length and width) at higher leaf saturations, with the widest apertures in saturated leaves. In *S. acaulis* and *S. bronchialis*, stomatal was steadily reduced in a similar pattern until the stomata closed after about 2.5 hours of drying-out. For *S. caespitosa*, stomata were suddenly closed after about 1.5 hours without apparent partial closure. In the three species investigated, total stomatal closure have occurred after about half to one hour of "apparent" stomatal closure on the drying-out curves. The pattern was however very similar in both drying-out curves and stomatal aperture curves.

Water Loss from Cut Shoots

The range of average values for the amount of water content lost in 24h (Table 8.2) was from 47% in *P. uniflora* to 82% of saturated water content in *S. bronchialis*, while the values for the percentage of fresh weight lost (this can be due to water loss, respiration, loss of volatile compounds, etc.) ranged from 43.9% to 78% of initial fresh weight in the same species, respectively. There was, however, a tendency for all species to retain their leaf shape and to lose less of their fresh weight than water content, with the exception of *E. androsaceum* which lost more of its fresh weight than its saturated water content.

Table (8.2): Initial percentage water contents (based on fresh weight), and the percentages of initial fresh weight and water losses over 24 hours. Standard deviation in brackets.

Species	% initial water content	% loss of the water content	% loss of fresh fresh weight	n
Eriogonum androsaceum	76.5(2.2)	69.0(0.25)	75.4(2.6)	4
Potentialla uniflora	61.7(1.9)	47.0(0.10)	43.9(1.6)	5
Saxifraga caespitosa	78.6(2.8)	76.4(0.20)	71.4(2.5)	4
Saxifraga bronchialis	81.0(1.1)	82.0(0.10)	78.0(1.5)	5
Silene acaulis	78.9(0.8)	59.7(0.03)	45.1(0.9)	5
Dryas octopetala	62.6(1.7)	64.7(0.02)	43.8(1.8)	5

The leaf edges of some species such as *D. octopetala* were curled towards the lower side of the leaf.

It should be noted that the death of excised shoots occurs faster than the death of an individual plant as a whole which has greater ability to withstand dry conditions and to resume normal functioning after severe dehydration.

Anatomical Measurements

The results for the different species are summarized in Table(8.3). The average external surface areas of the leaves utilized in the anatomical measurements are also presented. From these data it is possible to draw up a useful picture of the structural features of the studied plants.

(A) Specific leaf area (SLA), thickness of lamina and cuticule and leaf volume - The average specific leaf area ranged from 1.74 $mm^2.mg^{-1}$ in *S. bronchialis* to 3.17 $mm^2.mg^{-1}$ in *P. uniflora*. The remaining species had intermediate values.

The lamina thickness of the species studied ranged from 125-682 µm. It was greater in the three species with succulent leaves; *S. bronchialis*, *S. caespitosa* and *S. acaulis*. The mesophyll of these three species is undifferentiated into palisade and spongy portions, but consists of rounded cells, those towards the centre of the leaf being slightly larger.

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Table (8.3): Anatomical features of the leaves of the investigated cushion plants. Standard deviation in brackets (n=50). 1 = External leaf surface area (cm²); 2 = Specific leaf area (mm²/mg); 3 = Thickness of lamina (μ); 4 = Thickness of outer epidermal wall (μ): a-Upper epidermis, b-Lower epidermis; 5 = Leaf volume (cm³); 6 = Leaf volume / external surface area; 7 = Relative conducting area (mm²/g fresh wt): a-Stem, b-Leaf; 8 = Stomata density (number / mm²): a-Upper epidermis, b-Lower epidermis; 9 = Stomatal length (μ): a-Upper epidermis, b-Lower epidermis; 10 = Stomatal index: a-Upper epidermis, b-Lower epidermis; 11 = Hair cover (+++ very dense).

Character	Eriogonum androsaceum	Potentilla uniflora	Saxifraga caespitosa	Saxifraga bronchialis	Silene acaulis	Dryas octopetala
1	00.25(0.05)	00.37(0.08)	00.12(0.03)	00.07(0.03)	00.07(0.02)	00.59(0.10)
2	2.18(0.25)	3.17(0.40)	2.68(0.15)	1.74(0.18)	3.09(0.50)	2.68(0.22)
3	312(27)	125(13)	406(15)	682(15)	426(26)	253(18)
4a)	5.8(0.8)	5.1(0.8)	3.2(0.8)	6.8(1.1)	9.9(1.0)	7.7(1.4)
b)	2.7(0.3)	2.5(0.4)	4.7(1.2)	11.0(2.4)	9.8(1.4)	2.7(0.3)
5	0.68(0.2)	0.40(0.1)	1.10(0.3)	1.20(0.1)	1.30(0.2)	0.68(0.2)
6	2.7(0.3)	1.1(0.2)	9.1(1.2)	17.0(2.5)	18.9(2.6)	1.2(0.2)
7a)	0.5(0.11)	1.0(0.20)	0.2(0.03)	0.1(0.06)	0.6(0.15)	0.5(0.05)
b)	0.07(0.01)	0.06(0.01)	0.04(0.02)	0.04(0.01)	0.09(0.01)	0.10(0.01)
8a)	144(14)	————	198(13)	148(17)	361(27)	————
b)	210(25)	766(42)	45(06)	140(12)	133(16)	241(21)
9a)	32.8(2.79)	————	30.2(1.83)	33.5(2.11)	29.6(1.96)	————
b)	29.4(1.00)	27.2(2.67)	39.3(3.69)	33.5(1.63)	36.8(2.99)	19.8(1.60)
10a)	16.9(0.69)	————	16.3(3.50)	13.7(0.92)	29.2(1.20)	————
b)	18.3(1.20)	22.3(2.98)	06.1(0.80)	11.3(1.63)	14.5(1.90)	12.9(2.48)
11	+++	+++	+	+	+	+++

The two species *P. uniflora* and *D. octopetala* possessed the lowest leaf thickness. The mesophyll was well-differentiated into palisade and spongy (bifacial leaf) portions. The palisade tissue occurs towards the upper surface of the leaf and consists of 2-3 layers of elongate compact cells that occupy one-half to two-third of the leaf thickness. The spongy tissue is formed of loosely organized cells. In the remaining species, *E. androsaceum*, the mean thickness of lamina was 312 µm. The mesophyll has two upper and two lower palisade layers (isobilateral mesophyll) enclosing one layer of spongy cells. The palisade is present alone on peripheral areas of the blade. Spherocrystals (druses) of calcium carbonate may exist in the spongy cells.

The thickness of the outer wall (cuticle) of the upper epidermis in different species ranged from 3.2 to 9.9 µm and from 2.5 to 11.0 µm on the lower epidermis. In the three species with succulent leaves, the outer wall of the lower epidermal cells tends to be thicker than that of the upper epidermis. The opposite is true for the remaining three species *E. androsaceum*, *P. unflora* and *D. octopetala*, where the thickness of the outer wall of the upper epidermal cells is more than twice that of the lower epidermis.

Leaf volume ranged from 0.68 cm^3 in *E. androsaceum* and *D. octopetala* to 1.3 cm^3 in *S. acaulis*. It reached only 0.4 cm^3 in *P. uniflora*. It tends to be greater in the species with succulent leaves which also possess the least external surface area. The external leaf surface area of *D.*

octopetala, *P. uniflora* and *E. androsaceum* was larger in relation to the leaf volume than in the other smaller-leaved species. The leaf volume/surface area ratios are highest in the three species with succulent leaves where it ranged from 9.1 to 18.9, while in the remaining three species the ratios were relatively low, ranging from 1.1 to 2.7. In all species, the leaf volume/surface area ratio was greater than one. This is considered to be an adaptation which decreases the external surface area (transpiring surface) with respect to the internal volume of the leaf.

(B) Relative conducting area - The relative conducting area, which is the sum of the cross-sectional areas of all xylem elements expressed with reference to the mass of the plant parts supplied, is a measure of the ease with which the individual shoot components of a plant can be supplied with water. Relative conducting area not only varied among different species but also within a single species. It ranged from 0.11 to 1.00 in stems and from 0.04 to 0.10 in leaves.

(C) Stomata - The number of stomata per unit area (density) varied considerably from species to species. In four of the six species, stomata occur on both surfaces (amphistomatous) of the leaves, but were usually more abundant on the upper (adaxial) surface. *E. androsaceum* ,however, has more stomata on the lower (abaxial) surface. They occur only on the lower surfaces (hypostomatous) of the leaves of the remaining two species (*P. uniflora* and *D.*

octopetala). The latter two species have higher stomatal density on the lower leaf surface than the amphistomatous species. Stomatal density ranged from 144 to 361/mm² on upper leaf surfaces and from 45 to 766/mm² on lower surfaces.

Mean stomatal lengths ranged from 29.6 to 33.5 µm on the upper surface and from 19.8 to 39.3 µm on the lower surface of the leaves, depending on species. In amphistomatous species, the stomata were generally longer on the leaf surface with lower stomatal density. The longest stomata were found on the lower leaf surface of *S. caespitosa* (39.3 µm), which possessed the lowest stomatal density (45/mm²) on its lower leaf surface. In *S. bronchialis* with similar stomatal density on both leaf surfaces, stomatal lengths were nearly identical on both surfaces. The stomata in amphistomatous species were longer than stomata of hypostomatous species.

Stomatal indices varied between 13.7 to 29.2 and 6.1 to 22.3 on both upper and lower leaf surfaces respectively. In amphistomatous species, the stomatal indices tend to be higher on the leaf surface with the highest stomatal density. In some species (e.g. *S. acaulis* and *P. uniflora*), stomatal indices showed the same sequence relationship with other species as the stomatal densities. This suggests that differences in stomatal densities and indices among species are dependent on environmental influences on stomatal differentiation as well as the plant species.

(D) Trichomes - A dense covering of hairs was found in *E. androsaceum*, *P. uniflora* and *D. octopetala*. This is assumed to increase boundary layer resistance and hence decrease evaporation. The species with dense cover of hairs are characterized by higher rates of transpiration, while species with less hair cover manage quite adequately without a dense hair cover. Furthermore, hairs may serve other purposes, such as scattering incoming radiation or breaking up soil-reflected radiation and/or may prevent insect attack and help to cool the leaf by increasing the total radiating surface.

D. Discussion

Water Relations

The importance of plant water relations in alpine/arctic regions particularly cushion-plants has been emphasized by Heilborn (1925), Spomer (1964), Sveshnikova (1973), Courtin and Mayo (1975), Addison (1977), Izmailova (1977), Koerner and DeMoraes (1979). Other authors (Slatyer 1967, Larcher 1980a and Kramer 1983) have stressed the importance of knowing the interrelationships between plant water content, transpiration, water saturation deficit and water potential in order to understand the water relations of a species. As a whole, the water relations of the species studied indicate that cushion plants are characterized by high values of transpiration, high water deficit and low water potentials. These characteristics suggest that cushion plants could be termed xerophytes.

The measurements of water content revealed that despite the fact that cushion plants are incapable of reducing their water loss to a great extent, they maintain high water content which decrease gradually when temperature increases. This result can be achieved only if the plants are able to extract water from the soil rapidly enough to compensate for water loss. The living plant material of the species studied contained from 50 to 84% average water content. Differences in water content between W and NW individuals were in the order of 3 to 9%, which is relatively small. This indicates a relatively stable water relations even under water stress conditions. There are three types of water content fluctuations over the temperature range (between 5 and 30°C):

1. The water content curves of W and NW plants are more or less parallel, with constant differences between highest and lowest values in W and NW individuals per species. *S. caespitosa* had a fluctuation range of 7. This indicates better internal control of water content than that shown by the other species.
2. Species with a wider range of water content fluctuations in W plants than in NW plants. *D. octopetala* and *E. androsaceum* had ranges of 22(W)/10(NW) and 11(W)/10(NW), respectively.
3. Species with a wider range of water content fluctuations

in NW plants than in W plants. *Potentilla uniflora*, *Silene acaulis* and *Saxifraga bronchialis*, had ranges of 20(NW)/16(W), 13(NW)/11(W), and 17(NW)/7(W) respectively.

The transpiration rates were intermediate compared to values given by other authors for alpine plants (Mooney et al. 1965 and 1968, Sveshnikova 1973, Courtin and Mayo 1975), while some species (*Saxifraga* spp.) showed lower transpiration rates. Tranquillini (1964) pointed out that among alpine plants, there are those with high as well as with low transpiration rates, and this is true even among cushion plants, a group having very uniform physiognomy.

Transpiration of cushion plants is characterized by large fluctuations over the temperature range of 5 to 30°C. The steady increase in transpiration of most species at lower temperatures can be considered a side effect of the adaptation of the photosynthesis complex to the short growing season. The stomata remain open at low temperatures, allowing continuous CO_2 uptake. This may be at the expense of the plant's water balance. However, despite large fluctuations in transpiration rates within and among species with temperature change, water content, WSD, and water potential hardly change at all.

As pointed out in Chapter IV, all the species have well developed root systems. An ecological advantage of this is the ability to replenish the large amounts of water lost through transpiration. Difficulties connected with water conduction have been met by specific features of cushion plants. The stems are short and very well insulated by a mantle of dry leaves below the active surface of the compact canopy. Since the cushion plant loses less heat by outward radiation than the surface of open soil, the insulated stems are warmer than the surroundings. Hence, water transport is expected to proceed uninterrupted.

It is apparent that transpiration shows stronger dependence on temperature than the other water relations parameters. The apparent increase in the rate of transpiration with increased temperature results mainly from an increase in the vapour pressure gradient between the leaf surface and the ambient air (Slatyer and Bierhuizen 1964). Other possible reasons for this increase are alternation in the cuticular resistances (Moreshet 1970) and temperature mediated stomatal opening (Baig and Tranquillini 1980). With the closure of stomata at high temperatures (above 25°C), transpiration decreases.

The average water potentials measured in this study were in the range from -8 to -25 bar for different species. The three species with succulent leaves (*S. acaulis*, *S. bronchialis* and *S. caespitosa*) showed a tendency to higher water potential, with values of more than -15 bar. This may be due to higher water content, differences in rooting patterns or differing transpiration rates. Some authors reported lower or higher water potential values than these reported here for alpine and cushion plants (Heilborn 1925, Sveshnikova 1973, Ehleringer and Miller 1975a, Courtin and Mayo 1975, and Izmailova 1977). Korstian (1924) pointed out that lowest water potential usually occurs on the most adverse sites and in more drought resistant species which differ in their tolerance to low water potentials.

Despite similarities in distribution all along the windward side (SW), *E. androsaceum* showed lower water potentials than *P. uniflora*. This can be attributed to the higher transpiration rates of the former. Courtin and Mayo (1975) and Addison (1977) reported that cushion plant water potentials tend to be high under conditions of high soil water potential. Koerner and DeMoraes (1979), and Spomer (1964) pointed out that soil moisture does not seem to play a restrictive role, because of the amount of water stored in the cushion plant packing material. This storage water may be available to the plant for more than three weeks even after cutting the plant from its main root (Rauh 1939). The examination of the watered versus non-watered plants shows, however, that the very small differences in water potential are enough to trigger considerably different physiological responses. Non-watered plants had reduced transpiration to a great extent at any temperature tested. These findings agree with Mooney (1982), who worked on a group of Mediterranean plants.

Water saturation deficits develop during periods when water losses exceed absorption. The manner in which they develop is complex. Plant growth is reduced more often by water deficits than by any other factor (Kozlowski 1968 - 1983). Cushion plants can handle relatively high WSDs. Average values ranged from 17 to 62%.

In all species, an increase in water deficit occurred during the period it took stomata to close completely (closure phase). WSD at the end of stomatal closure was as high as four times the WSD at the beginning of stomatal closure in *D. octopetala*. The rise in water deficit during the period of stomatal closure has been noted by many authors (Hygen 1953, Pisek and Winkler 1953, Slavik 1958, El-Sharkawy and Hesketh 1964, Hellmuth 1968 and Kramer 1983). The sensitivity of the stomatal mechanism and the rapidity of closure in *S. caespitosa* at the relatively low WSD of 7.6% appears to contribute to the plant's drought resistance. This is due to the fact that stomatal closure occurs sooner and more completely as water stress develops. In the other species, during the time lag between the first and second inflexion of the drying-out curves, a different type of pattern for transpiration occurs under such conditions of high stomatal resistance (usually small stomatal aperture of less than 2 µm). In this stage low rates of transpiration are expected due to stomatal movement. Okali (1971) and Nazrul-Islam (1983) suggested that species with a low degree of drought tolerance are expected to possess high stomatal sensitivity as an adaptation against the development of damaging water potentials. A low degree of drought tolerance with lower water deficits at the end of stomatal closure was found in *Saxifraga bronchialis, Saxifraga caespitosa* and *Silene acaulis*. The remaining three species can be considered more drought tolerant. Williams (1950) pointed out that epidermal modifications serve to maintain epidermal turgidity and thus enable the stomata to keep open over a wide range of internal water deficit. The behaviour of *Eriogonum androsaceum, Potentilla uniflora* and *Dryas octopetala*, as recorded in this study, supports William's contention.

It is generally believed that after complete stomatal closure, the moist boundary layer of the leaf will be reduced (Baig and Tranquillini 1980, Sowell et al.1982) depending on wind speed. Alpine cushion plants may reduce their boundary layer quickly. Cuticular transpiration accounted for 0.6 to 5% of the total transpiration.

Leaf temperature under controlled environmental conditions ranged from 4°C above to 2°C below air temperature. This can be attributed to particular physical features and morphological characteristics, such as:

1. The hemispherical growth-form reduces the surface/volume ratio of the plant which reduces energy loss (Hedberg 1964, Ralph 1978, Koerner and Cochrane 1983).
2. The low heat conductivity, where little energy is transferred or dissipated from the plants to their surroundings (Molgaard 1982, Fischer and Kuhn 1984).
3. The dead material (packing material) accumulated in the cushion plant body provides excellent heat storage.

4. The cooling effect of transpiration is small when compared to radiation intensity due to the angle of incidence (Clum 1926a and b).

However, a potential for overheating goes hand in hand with these features. The cushion's interior has a low heat conductivity which may lead to high surface temperatures. However, Martin (1943), Gates (1968) and Smith (1978) found that smallness of the leaf blade reduces overheating. Also, smallness of the leaves leads to relative reductions in transpiration (Smith and Geller 1980), consequently increasing water use efficiency (amount of water lost per dry matter produced).

Ecological Significance of Leaf Anatomy

The literature on ecological plant anatomy is surprisingly extensive, despite the fact that the science of ecology is a relatively late arrival to the field of botany (Mortenson 1973). The present results show that cushion plants are adapted to a wide spectrum of environmental conditions. This is reflected by anatomical features of the leaves: In small, thick leaves palisade tissue may be strongly developed, or may be totally absent. The lamina and cuticle may be very thick, or thin as in many mesophytic species. Stomatal densities and indices and the relative conducting areas vary across a broad range. Stomata are found on both sides of the leaf, or on the lower sides only. These variations in leaf anatomical characteristics have a direct and profound influence on plant water relations and gas exchange (Maximov 1931, Lewis 1972, van Volkenburgh and Davies 1977). Other authors (Forsaith 1920, Au 1969, Carlquist and Bissing 1976, Nautiyal and Purohit 1980) have demonstrated that the alpine environment plays an important role in promoting particular structural features, which may manifest themselves either as augmented or reduced structures. According to Carlquist (1987, pers. communication) alpine plants have up to 70% similarities to desert plants in their anatomical features. According to the widely accepted criteria for xeromorphy as reviewed by Shields (1950), Fahn (1964), and Mortenson (1973), some of the cushion plants on Mt. Allan belong to this group.

Differences in specific leaf area (SLA) are related to differences in both leaf thickness and volume. Also, Woodward (1979) pointed out that the temperature of the leaf may control SLA. Reduction in leaf volume is a feature correlated with reduction in the rate of transpiration, and plants with small leaves are more common in xeric habitats (Stocker 1960). Since most cushion plants possess small leaves, this offers better water economy in that all parts of the mesophyll are within a short distance. This is reflected by the high ratio of leaf volume to its external surface area. It is known that leaves with a well-developed palisade tissue transpire and photosynthesize more due to their increased internal surface area (Thoday 1931, Turrell 1936 and 1944, Shields 1950). This contention is supported by the high transpiration rates of *E. androsaceum* and *P. uniflora*, which possess palisade tissue occupying more than half of the leaf thickness.

The thick cuticle might conceivably afford protection against the effects of excessive radiation as well as of excessive transpiration. It has also been suggested that a thick cuticle protects the inner parts of the leaf from ultraviolet radiation, acts to protect the leaf against the mechanical action of wind, and helps to prevent the leaf from collapsing when it has lost water. Buckley et al. (1980) pointed out that the thick cuticle and high ratio of leaf volume to its external surface area are related to excessive wind speeds, excessive ultraviolet radiation, and the desirability of raising leaf temperature in sunny spells by cutting down transpiration. It is apparent that the cuticle is better developed or thicker on the leaf surface (upper or lower) that is oriented towards the sun. For example, it is very thick on the lower surfaces of *S. bronchialis* and *S. caespitosa* which are more oriented towards the sun. In most of the other species, the cuticle is thicker on the upper surfaces which again face the sun directly. Stalfelt (1956) pointed out that thickened outer walls of the epidermal cells are correlated with cold temperatures more often than with a lack of moisture.

As shown by Huber (1956), Larcher (1980a) and Kramer (1983), the relative conducting area is large in plants that transpire very strongly. Some desert plants have values of 2 to 3 $mm^2.g^{-1}$, and herbaceous sun plants with values between 1 and 2 $mm^2.g^{-1}$ were found. Most woody plants, hydrophytes and succulents have conducting areas less than 0.5 $mm^2.g^{-1}$. For cushion plants, the relative conducting area can be as low as in water plants or as high as in many herbaceous sun plants. The smaller relative conducting area in leaves than in the stems of the studied species is of great importance in limiting excessive water loss particularly under adverse conditions. However, not every plant is built like this. Kramer (1983) reported that relative conducting area in erect plants increases from bottom to top of the stem and is higher for the branches than for the main stem, so that the shoots at the top are at an advantage. Water in leaves is conducted not only by vascular tissue but also by the mesophyll cells, and water transport is much higher through palisade tissue than through the spongy tissue. Species with well-developed palisade tissue as *E. androsaceum* and *P. uniflora*, possess high rates of transpiration; the transport from the vascular bundles towards the epidermis is enhanced.

The results of stomatal counts indicate that there is no clear correlation between stomatal densities, indices and lengths, and the local distribution of species. Only *E. androsaceum*, *P. uniflora* and *D. octopetala* have more stomata and higher stomatal indices on the lower epidermis than the other species. Other researchers reported a decrease in the stomatal density, index and length with altitude (Au 1969, Koerner and Mayer 1980, Nantiyal and Purohit 1980). This behaviour is to provide a beneficial effect on water use efficiency (Ajiri et al. 1973, van Volkenburgh and Davies 1977). High density of stomata and high stomatal indices reduce the efficiency of stomatal control of vapour diffusion (Pospisilova and Solarova 1980, Koerner et al. 1983). This agrees with the present study, where the highest densities and indices occur in plants with high transpiration rates. However, the increase in number of stomata enables a higher rate of gas exchange under conditions of favourable water supply.

As reviewed by Parker (1968), stomata in rather drought-resistant plants close more rapidly than in less resistant ones. On the other hand, many drought resistant plants keep their stomata open longer than some less resistant ones. *D. octopetala* and *E. androsaceum* kept their stomata open for a longer time than the other species during drying-out of the cut shoots. According to the results, stomatal closure is directly related to a slowing, but not necessarily to a complete cessation of transpiration. Cuticular transpiration is great in some species. In the meantime, photosynthesis may decline at a different rate than transpiration as stomata close (Larcher 1963 and 1980a, and Nobel 1980).

The dense hair cover on the leaves of some species may provide protection against excessive solar radiation and the desiccating effects of dry winds which prevail in their habitats. Despite being inferior to the cuticle in reducing transpiration, trichomes on leaves may retard transpiration during windy and sunny periods before the cuticle is fully developed. Possibly trichomes are symptoms of excessive water loss rather than structures which function in minimizing it (Shields 1950). Others (Ehleringer and Mooney 1978) have shown that pubescence reduces leaf absorbance resulting in a reduced heat load, which results in lower leaf temperature and transpiration rates. There is a disadvantage associated with leaf pubescence. By reflecting quanta that might otherwise be used in photosynthesis, the presence of leaf hairs reduces the rate of photosynthesis. In agreement with other studies (Fahn 1964 and Mortenson 1973), trichomes and thick cuticle have little value in reducing transpiration as long as stomata are open, but when stomata close, these features appear to fulfill an important protective function.

Species Distribution

The role of water relations in the local distribution of alpine cushion plants is an intriguing question, but difficult to answer completely. The factors involved in limiting the altitudinal distribution of high mountain plants have been the subject of limited experimentation as well as of conjecture (Mooney et al. 1965). Many factors in addition to adult morphological and physiological characteristics associated with water relations are important in influencing species distribution (Barnes and

Harrison 1982). Temperature and water stress affect many plant processes, though one of the earliest and most recognizable responses is the closure of stomata. This mechanism allows for a reduction in transpiration, yet it also reduces photosynthesis. *E. androsaceum*, *P. uniflora* and *D. octopetala* showed higher transpiration rates than the other three species, and that will not limit their photosynthesis, as the stomata are open. Also their ability to handle relatively lower water contents, high WSDs, and lower water potentials together with their extensive root systems, ensure that they can delay the onset of water stress and maximize the period of growth and distribution.

It is evident that water relations play some part in the altitudinal distribution of cushion plants. At distributions beyond the natural range of the species, transpiration can exceed water absorption even from moist soils, resulting in injury or death (Barnes and Harrison 1982). However, Mooney et al. (1968) and Sveshnikova (1973) pointed out that there is no relationship between the zonal position of a plant as such, and the intensity of its transpiration.

E. Conclusions

Stability of the water budget can be attained by mountain cushion plants as follows:

1. More efficient water absorbing system.
2. Uninterrupted water movement through the plant organs.

3. Better control over water loss.
4. Water storage in the packing material.

For all species the well-developed root system and considerable water reserves in the roots and in the packing material are common. It appears that species segregation exists with respect to water regime. One may recognize two extreme behavioural mechanisms in cushion plants: 1) Widely distributed species are unable to restrict water loss to a great extent (having late gradual stomatal closure), with a high rate of transpiration and low water potential. The WSD is relatively high, which induces stomatal closure, a mechanism of great value for gas exchange. (e.g. *Eriogonum androsaceum* and *Potentilla uniflora*). The low water potential increases the ability to extract water from relatively dry soil and to compete with other xeric species. 2) The narrowly distributed species which are able to restrict water loss greatly (having early simultaneous stomatal closure), with a low rate of transpiration, and higher water potential. The WSD is low, inducing early stomatal closure (e.g. *Saxifraga caespitosa*).

Other species adopt an intermediate strategy.

F. Summary

The results obtained in this study are:

1. Cushion plants are capable of maintaining a high average water content ranging from 50 up to 84%. This behaviour can be achieved by low water potentials and rapid

extraction of water from the soil.

2. Despite the large fluctuations in transpiration rates with temperature within and between species, plants hardly change their water content, WSD, and water potential. This indicates good internal control of the water regime.
3. At temperatures below 20°C, transpiration depends to a large extent on temperature, that is, on the differences in vapour pressure deficit between the leaf and the ambient air. At temperatures above 25°C transpiration is controlled mainly by stomatal activities.
4. The average water potentials of various species covered a wide range from -8 to -25 bar, and they correlate with the other water relation parameters. This indicates that cushion plants can establish a stable and high water supply, as long as some water is available in the soil.
5. Some species were characterized by high water saturation deficits. The stomatal response and speed of closure when water deficits rise appear to contribute to the drought resistance of these plants.
6. Cushion plants attain higher leaf temperatures than the surrounding environment. This is attributed in part to their particular features. The large leaf/air temperature differences allow high transpirational flux even when the atmosphere is saturated with water vapour.
7. Cushion plants are adapted to different environmental conditions. This is reflected in the anatomical features

of the leaves. Some have small, thick leaves with the palisade tissue strongly developed or totally absent. Some mountain cushion plants have relatively large, thin leaves with low leaf volume/external surface area ratios. The lamina and cuticula may be very thick or thin. The stomatal indices and the relative conducting areas vary in a broad range. The stomata are found on both sides of the leaf or on the lower side only.

8. These different properties position each species between two extremes: a) The widely distributed species (e.g. *E. androsaceum*) are less efficient in their ability to restrict water loss, with high rates of transpiration, low water potentials, and relatively high WSD. b) The narrowly distributed species (e.g. *S. caespitosa*) are more efficient in their ability to restrict water loss, with low rates of transpiration, higher water potential, and lower WSD.

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IX. General Discussion

A. Conclusions

Hypothesis 1

The rooting and resource allocation patterns of cushion plants with the same aboveground form are different and site dependent.

The results of the root studies support this hypothesis. Differences in rooting patterns were demonstrated in root configuration, horizontal extension, and depth. For widely distributed species, there was a definite trend towards deep root penetration in the lower slope site and less penetration in the ridge and crest sites. The opposite happened with respect to horizontal root extension. Where moving soil (gravel, rocks) occurs, roots are one sided, holding the cushion plant in place. New cushions may sprout from the exposed roots or rhizomes. producing an altitudinal sequence of cushions with the older ones at the lower place. The site-dependent differences of rooting pattern are related to a variety of topographic, microclimatic, and edaphic factors.

Regarding the resource allocation pattern, the hypothesis is strongly supported. Two main types of site dependency were identified: "Pioneer" cushions on unstable slopes and "climax" cushions on stable sites. Both types had higher vegetative reproduction allocation than sexual reproductive allocation, showing that a specific and unusual succession takes place on such sites.

Hypothesis 2

The growing season for alpine cushion plants is longer than that of other vascular plants of this region.

This hypothesis can only be partially considered true. Mountain cushion plants have the ability to modify their microclimate and to keep plant temperatures higher than ambient air temperature, even in autumn. But the endogenous phenological rhythm overrides environmental parameters. The leaves senesce in late summer anyway, irrespective of good or bad conditions. The affect of the better temperature regime within the cushion in promoting root growth and development of overwintering buds in the fall, has not been investigated in this study.

The second leaf flushing shown by some species towards the end of some summers can be considered as a secondary adaptive strategy to compensate for late summer senescence. This enables the plants to utilize more efficiently, favourable periods in the autumn. This indicates that late summer senescence in cushion plants does not always mean the end of the photosynthetic period.

Hypothesis 3

Seed germination and seedling establishment play an important role for the distribution of alpine cushion

plants.

This hypothesis appears to be true for most of the species investigated. Seedlings are rare in natural alpine habitats. The rapidity of germination and seedling growth may account for the success of some cushion plants in becoming established under the alpine conditions.

Hypothesis 4

Net photosynthesis is rather low, while the rate of respiration is relatively high.

This hypothesis was proven true. Photosynthesis and respiration demonstrated the physiological adaption of the species to temperature and light intensity experienced at high altitude. The data suggest that cushion plants have greater heat and lower light requirements than most alpine plants. Rates of respiration are high. This may allow respiration to exceed photosynthesis under certain conditions. The high rates indicate the ability for rapid metabolic activity.

Hypothesis 5

The plant water relations of a species with a wide range of distribution are different from those of a species with a narrow range of distribution.

This hypothesis is well supported by the results. The differences between local distribution of the species are in part a consequence of differences in water use patterns, which are themselves a consequence of differences in leaf structure, genetic makeup and plasticity, phenology and physical habitat.

Large fluctuations in transpiration rates do not alter water content substantially. The water regime is kept rather stable. The widely distributed species are characterized by higher transpiration rates, lower water contents, lower water potential, and higher water saturation deficits. This together with the extensive root systems ensure that these plants can delay the onset of water stress and maximize the period of growth. The ability of widely distributed species to transpire at low temperatures enable the plants to extend their distribution to high elevations. In contrast, narrowly distributed species are able to restrict water loss greatly by early simultaneous stomatal closure.

Hypothesis 6

The relationship between cushion plants and their habitat is primarily a matter of survival and tolerance instead of perfect adaptation.

Within the large altitudinal gradient on every high mountain, smaller environmental gradients play an important role. Only few plants are able to invade steep, windy, unstable rocky slopes; cushion plants can do it. But their existence in this particular harsh habitat is an ongoing struggle for survival. It begins with fast seed germination, is dramatically demonstrated by rare seedling establishment and ends often enough in the physical destruction of mature cushion by rockfall and solifluction. The study revealed a number of tolerance mechanisms, developed in cushion plants, enabling them to cope better with unfavourable conditions than other vascular plants can do.

B. Summary

Six species of vascular plants are the common cushion plants on Mount Allan. They belong to four different families and they are unevenly distributed between 2000 and 2400 m above sea level (Fig. 2.4). Along this altitudinal gradient several micro habitats occur with differences in aspect, slope, soil development, moisture, wind, radiation, temperature, plant cover, animal activity, human impact etc.

Eriogonum androsaceum and *Potentilla uniflora* are flexible in their requirements and both occupy a variety of different habitats on the south-west side of the mountain (local "widely distributed" species).

In contrast to these two species *Dryas octopetala* is dominant on the north-east side of the mountain.

Saxifraga caespitosa, *Saxifraga bronchialis*, and *Silene acaulis* are relatively restricted in their distribution with different degrees of flexibility. As compared to these three species, the local widely distributed cushion plants have the following characteristics:

1. Ability to modify their phenological behaviour.
2. Well-developed root systems with plastic response to

site variation.

3. High seed germination values.
4. Higher photosynthesis and respiration rates. Higher light compensation and saturation points. Lower temperature minima, optima, and maxima for net photosynthesis.
5. Lower dry matter allocation to sexual reproduction.
6. Lower efficiency in water loss restriction. Higher rates of transpiration, lower water potential, and higher water saturation deficit. More xeromorphic features.

X. Appendix

Legend:

C = °C

mg Co2.g Dw.h = mg $CO_2.g^{-1}.DW.h^{-1}$

mg Co2.dm.h = mg $CO_2.dm^{-2}.h^{-1}$

mol.m.sec = $\mu mol.m^{-2}.sec^{-1}$

Appendix(1): Soil moisture content(% air dry weight)at successive depths in the different sites of the study area. Each value represents a mean of three samples.

Depth (cm)	SW-side Lower slope	 Upper slope	Ridge	Crest	NE-side
June 21, 1983:					
00-05	11.2	08.1	05.6	05.1	17.5
06-10	13.2	10.6	10.5	08.3	30.1
11-20	16.1	13.2	14.7	13.8	41.5
21-30	19.4	14.3	16.1	17.0	43.2
July 5, 1983:					
00-05	09.1	05.3	04.3	04.1	14.6
06-10	10.3	08.7	09.5	06.7	25.7
11-20	12.5	09.2	11.2	10.9	38.8
21-30	15.7	09.5	12.9	12.9	40.1
August 15, 1983:					
00-05	01.1	00.8	01.0	01.1	02.1
06-10	03.5	02.5	03.2	02.2	09.4
11-20	06.7	03.3	04.2	03.8	12.0
21-30	06.8	04.2	05.1	05.5	15.2

Appendix(2): Daily course and average wind velocity(m/sec) with height aboveground(cm) at time of measurements on both south-west and north-east sides of Mt Allan. Values are means of five readings.

Height aboveground (cm)	Time of the day(hour) 7 SW	 NE	 10 SW	 NE	 14 SW	 NE	 18 SW	 NE	 21 SW	 NE	 average SW	 NE
July 5, 1983:												
10 cm	1.1	0.0	03.4	0.6	02.3	0.5	03.8	0.5	0.9	0.0	2.3	0.3
25 cm	1.2	0.2	06.1	0.7	03.2	0.6	05.3	1.5	1.8	0.0	3.5	0.6
50 cm	1.7	0.5	06.9	0.9	04.0	0.8	06.6	2.1	2.7	0.3	4.4	0.9
200 cm	3.4	1.1	10.4	1.3	06.1	1.6	10.2	3.0	3.4	0.5	6.7	1.5
August 15, 1983:												
10 cm	1.5	0.2	02.7	0.4	06.9	1.2	05.2	0.8	3.1	0.3	3.9	0.6
25 cm	1.8	0.5	02.9	0.9	07.8	2.7	06.1	0.9	4.0	0.6	4.5	1.1
50 cm	2.4	0.8	04.7	1.0	11.0	2.9	08.8	2.0	4.6	0.7	6.3	1.5
200 cm	5.5	1.5	07.1	1.8	14.2	3.5	11.9	2.7	6.7	1.7	9.1	2.3

Appendix(3): Daily course of soil-cushion plant-air temperatures(C) at time of measurements on SW-side(Eriogonum androsaceum) and NE-side (Saxifraga bronchialis) of Mt Allan .

	Time of the day(Hour)									
	07		10		14		18		21	
	SW	NE	SW	NE	SW	NE	SW	NE	SW	NE
July 5,1983:										
Rhizosphere(-10cm)	15.1	12.3	16.8	16.4	18.9	18.0	19.2	13.5	16.5	13.2
bare soil surface	09.8	10.1	09.1	15.2	09.3	10.5	18.3	08.9	08.6	08.9
Plant canopy	09.8	13.5	12.5	12.8	21.5	12.5	22.5	12.3	15.5	10.4
Leaf surface	11.5	23.0	19.3	27.0	20.5	11.8	18.6	11.5	15.2	10.0
25cm aboveground	09.6	13.6	14.2	17.1	13.8	12.7	18.3	12.0	14.6	11.3
50cm aboveground	08.2	13.5	12.0	16.0	12.4	12.0	17.5	11.3	14.0	10.2
200cm aboveground	08.0	12.2	11.2	15.0	11.8	11.0	16.3	11.0	13.8	10.0
August 15,1983:										
Rhizosphere(-10cm)	18.0	18.5	18.4	20.6	18.7	22.5	19.5	21.5	19.1	20.2
bare soil surface	10.5	13.5	17.9	23.8	27.5	21.5	29.0	16.8	17.5	13.1
Plant canopy	09.4	12.0	09.8	17.1	13.2	17.6	13.9	14.9	13.0	14.5
Leaf surface	09.2	13.0	18.2	22.5	23.1	22.0	21.5	17.5	11.7	11.5
25cm aboveground	09.2	08.5	17.6	21.5	20.2	21.3	15.5	15.7	12.5	12.0
50cm aboveground	09.0	08.3	17.0	20.0	18.0	21.0	15.3	15.0	12.2	11.6
200cm aboveground	07.8	08.0	15.6	18.0	17.5	19.0	14.0	13.7	11.5	11.0

Appendix (4): Phenological measurements of the studied species at various sites. PI=phenological index, GL=number of green leaves per branch, DL=number of dying-back leaves per branch. Standared deviation in parentheses. 30 individual plants were observed per species at each site.

App.(4.A): In May 24,1984.

Phenological measurements	Study sites					
	I	II	III	IV	V	VI
Eriogonum androsaceum						
PI	1.2(0.1)	01.0(0.0)	01.0(0.0)	-----	-----	
GL	1.3(0.2)	00.0(0.0)	00.0(0.0)	-----	-----	
DL	0.0(0.0)	00.0(0.0)	00.0(0.0)	-----	-----	
Potentilla uniflora						
PI	1.3(0.2)	01.1(0.1)	01.0(0.0)	-----	-----	
GL	2.0(1.0)	00.5(0.2)	00.0(0.0)	-----	-----	
DL	0.0(0.0)	00.0(0.0)	00.0(0.0)	-----	-----	
Saxifraga caespitosa						
PI		01.3(0.2)		-----		
GL		02.1(1.0)		-----		
DL		01.5(0.8)		-----		
Saxifraga bronchialis						
PI		01.4(0.2)	01.4(0.2)	-----	-----	-----
GL		11.2(2.3)	10.5(2.0)	-----	-----	-----
DL		04.2(1.6)	04.5(1.5)	-----	-----	-----
Silene acaulis						
PI			01.0(0.0)		-----	-----
GL			00.0(0.0)		-----	-----
DL			00.0(0.0)		-----	-----
Dryas octopetala						
PI			01.0(0.0)		-----	-----
GL			00.0(0.0)		-----	-----
DL			00.0(0.0)		-----	-----

App.(4.B): In June 20,1984.

Phenological measurements	Study sites					
	I	II	III	IV	V	VI
Eriogonum androsaceum						
PI	3.5(0.2)	02.7(0.1)	02.6(0.1)	02.4(0.2)	02.3(0.1)	
GL	8.1(0.9)	05.9(0.3)	07.9(1.0)	06.5(0.4)	04.1(0.4)	
DL	00	00	00	00	00	
Potentilla uniflora						
PI	3.8(0.2)	03.6(0.2)	03.3(0.3)	03.3(0.2)	02.7(0.1)	
GL	5.8(0.7)	04.7(0.5)	05.3(0.3)	04.3(0.3)	03.4(0.6)	
DL	00	00	00	00	00	
Saxifraga caespitosa						
PI		03.4(0.2)		03.8(0.5)		
GL		12.7(1.3)		12.7(2.2)		
DL		02.0(0.5)		02.4(0.8)		
Saxifraga bronchialis						
PI		03.5(0.1)	03.4(0.3)	03.7(0.1)	03.2(0.2)	03.2(0.2)
GL		26.7(3.9)	27.1(4.0)	26.2(3.2)	22.5(3.3)	23.6(3.8)
DL		04.6(2.1)	04.8(1.6)	05.8(2.0)	06.0(1.5)	05.8(1.8)
Silene acaulis						
PI			03.4(0.3)		02.6(0.3)	02.5(0.1)
GL			07.8(0.9)		06.3(0.7)	05.2(1.1)
DL			00		00	00
Dryas octopetala						
PI			02.4(0.2)		02.2(0.2)	01.8(0.3)
GL			04.0(0.3)		02.9(0.3)	02.3(0.3)
DL			00		00	00

App.(4.C): In July 12,1984.

Phenological measurements	Study sites					
	I	II	III	IV	V	VI
Eriogonum androsaceum						
PI	3.9(0.1)	03.0(0.2)	03.1(0.4)	03.2(0.1)	02.6(0.1)	
GL	9.7(2.0)	10.3(1.2)	11.8(1.9)	09.8(0.6)	09.9(1.5)	
DL	00	00	00	00	00	
Potentilla uniflora						
PI	5.0(0.3)	04.6(0.4)	05.2(0.4)	05.0(0.2)	05.0(0.3)	
GL	5.8(0.9)	06.3(1.2)	05.9(0.4)	07.2(1.2)	06.1(0.9)	
DL	0.6(0.5)	00	00.9(0.5)	00.8(0.5)	00.7)0.4)	
Saxifraga caespitosa						
PI		05.2(0.2)		05.0(0.4)		
GL		16.8(1.6)		14.1(2.8)		
DL		04.2(1.2)		04.5(1.5)		
Saxifraga bronchialis						
PI		03.8(0.2)	03.9(0.2)	03.8(0.1)	03.8(0.2)	03.7(0.3)
GL		30.7(2.7)	25.6(4.0)	25.3(1.6)	27.4(4.2)	24.2(3.8)
DL		08.5(2.5)	07.4(4.6)	07.8(5.2)	05.9(3.0)	05.5(2.0)
Silene acaulis						
PI			05.2(0.1)		04.6(0.1)	03.4(0.2)
GL			08.4(0.6)		07.3(0.6)	11.8(2.8)
DL			00		00.3(0.2)	00
Dryas octopetala						
PI			05.4(0.2)		04.7(0.2)	03.6(0.2)
GL			04.9(0.8)		05.2(0.9)	04.7(0.5)
DL			01.3(0.4)		00.7(0.5)	00

App.(4.D): In August 24,1984

Phenological measurements	I	II	III	IV	V	VI
Eriogonum androsaceum						
PI	07.2(0.1)	07.3(0.1)	07.4(0.2)	06.5(0.4)	06.1(0.2)	
GL	12.9(3.4)	13.3(1.8)	11.3(2.3)	08.8(2.4)	10.7(3.2)	
DL	03.2(1.4)	03.3(0.8)	03.1(0.8)	03.3(0.6)	01.9(0.6)	
Potentilla uniflora						
PI	07.3(0.1)	07.3(0.1)	07.4(0.2)	07.2(0.1)	07.1(0.2)	
GL	05.7(1.4)	05.9(1.1)	04.5(0.7)	04.4(0.7)	03.4(0.6)	
DL	01.6(0.5)	02.0(0.5)	01.7(0.6)	02.0(0.5)	01.7(0.6)	
Saxifraga caespitosa						
PI		07.5(0.1)		07.4(0.4)		
GL		10.4(1.4)		12.0(1.8)		
DL		07.3(1.2)		06.1(0.9)		
Saxifraga bronchialis						
PI		07.3(0.1)	07.4(0.2)	07.0(0.2)	06.7(0.1)	07.0(0.2)
GL		20.7(3.0)	19.2(3.8)	25.9(4.5)	20.2(2.1)	27.0(4.0)
GL		12.3(2.9)	12.3(3.7)	09.7(2.8)	09.7(1.2)	04.2(1.9)
Silene acaulis						
PI			07.3(0.2)		07.0(0.3)	07,2(0.1)
GL			11.1(1.5)		10.4(1.2)	12.6(1.7)
DL			02.4(0.7)		03.8(0.6)	01.6(0.7)
Dryas octopetala						
PI			07.4(0.1)		07.3(0.2)	07.2(0.1)
GL			04.2(0.6)		03.6(0.8)	04.5(0.6)
DL			02.6(0.6)		02.2(0.4)	01.5(0.7)

Appendix (5): Number of flowering stalks produced per individual plants of different species during the growing season of 1984 . Standared deviation in parentheses (n=30).

Plant size class (sq.dm)	I	II	III	IV	V	VI
Eriogonum androsaceum						
<2	016.0(07.0)	06.5(01.5)	008.0(05.7)	08.3(03.9)	004.5(00.5)	
2-5	042.0(27.0)	22.5(10.5)	013.0(04.0)	14.5(05.2)	014.4(06.5)	
5-10	027.2(09.4)	21.5(09.2)	010.3(06.6)	22.5(17.5)	022.5(05.5)	
10-15	040.8(06.5)	34.0(06.0)	031.5(05.2)	33.5(04.5)	030.6(05.2)	
>15	084.6(20.3)	71.3(30.5)	078.5(35.5)	46.0(40.2)	045.6(36.2)	
Potentilla uniflora						
<2	016.7(05.5)	17.0(03.5)	009.0(04.0)	10.5(02.5)	014.0(04.3)	
2- 5	044.6(13.9)	36.8(07.4)	025.3(17.5)	19.7(08.1)	041.0(14.8)	
5-10	066.3(37.1)	57.5(10.2)	058.0(06.0)	31.0(02.9)	050.7(10.2)	
10-15	113.0(26.0)	89.3(24.1)	121.3(43.9)	55.0(15.0)	060.2(08.5)	
Saxifraga caespitosa						
<0.2		09.7(03.9)		08.5(02.6)		
0.2-0.5		11.5(02.3)		16.8(04.1)		
0.5-0.8		23.5(01.8)		27.7(02.1)		
0.8-1.0		29.6(05.4)		33.5(05.8)		
>1.0		35.0(07.2)		42.8(06.6)		
Saxifraga bronchialis						
<1		15.0(03.0)	014.8(06.2)	07.5(01.5)	007.3(03.3)	11.3(2.9)
1-2		21.5(08.5)	015.3(02.1)	14.8(03.4)	013.7(06.6)	15.5(1.5)
2-3		22.8(06.3)	026.5(02.5)	20.0(04.0)	029.2(03.3)	18.2(4.6)
3-4		28.0(06.5)	030.7(08.3)	25.5(05.5)	040.6(05.8)	20.4(2.5)
4-5		32.9(08.6)	034.0(07.5)	31.0(04.8)	058.4(06.2)	24.5(3.8)
>5		52.6(03.4)	048.3(06.5)	55.8(05.2)	054.2(08.3)	48.6(4.8)
Silene acaulis						
<1			022.0(06.0)		017.8(04.7)	08.8(1.3)
1-3			077.0(27.9)		026.5(14.5)	13.0(2.8)
3-5			079.5(12.2)		069.3(21.9)	23.6(2.2)
5-8			095.3(25.4)		087.6(15.5)	29.7(4.8)
Dryas octopetala *						
			138.0(66.0)		121.4(60.2)	166.5(93.8)

* number per square meter of plant carpets

Appendix (6): Germination and seedling growth of various species at different temperatures in dark(D), light(L), and alternating light and darkness(L/D) with 14 hr day. GV=germination value. (n=100 seeds).

App.(6.A): Eriogonum androsaceum.

Temp. (C)	Light treat.	% Germination after.........days									GV	Root length (mm)	Shoot length (mm)
		2	3	4	5	6	7	8	9	10			
10		00	00	00	00	00	00	00	00	00	0.00	00.0	00.0
15	L	00	00	00	00	00	03	03	03	03	0.13	04.6	05.8
	D	00	00	00	00	03	03	03	03	03	0.13	08.5	19.2
	L/D	00	00	00	00	00	00	00	00	00	0.00	00.0	00.0
20	L	00	00	00	00	00	00	03	03	03	0.11	05.1	03.5
	D	00	00	00	00	00	03	03	05	05	0.28	14.0	16.0
	L/D	00	00	00	00	00	03	03	03	03	0.11	02.6	00.0
25	L	00	00	00	00	00	00	03	03	03	0.11	05.5	09.8
	D	00	00	00	00	00	00	00	00	00	0.00	00.0	00.0
	L/D	00	00	00	00	00	03	03	03	05	0.25	06.3	05.6
30		00	00	00	00	00	00	00	00	00	0.00	00.0	00.0
35		00	00	00	00	00	00	00	00	00	0.00	00.0	00.0
20/10	L/D	00	00	00	00	00	05	05	08	08	0.71	06.8	05.5
25/15	L/D	00	00	00	00	00	03	03	08	13	1.69	07.5	05.8
30/20	L/D	00	00	00	00	00	00	03	05	05	0.29	07.5	05.4

App.(6.B): Potentilla uniflora

Temp. (C)	Light treat.	% germination after..........days									GV	Root length (mm)	Shoot length (mm)
		2	3	4	5	6	7	8	9	10			
10	L	00	00	00	00	00	00	05	05	08	00.64	01.0	00.0
	D	00	00	00	00	00	00	03	05	08	00.64	00.8	00.0
	L/D	00	00	00	00	00	00	08	10	10	01.11	01.2	00.0
15	L	00	00	00	00	00	03	10	25	27	07.50	01.5	00.0
	D	00	00	00	00	00	11	25	28	32	10.00	04.5	00.8
	L/D	00	00	00	00	10	20	38	38	40	19.00	02.0	00.5
20	L	00	00	25	65	70	73	73	73	73	81.67	17.2	02.7
	D	00	00	60	88	88	88	88	88	88	154.88	18.4	20.8
	L/D	00	00	33	68	75	75	75	75	75	96.82	27.6	02.4
25	L	00	23	58	60	68	75	78	78	78	88.40	16.5	02.0
	D	00	30	55	55	58	58	58	58	58	97.75	13.0	23.9
	L/D	00	43	65	73	73	75	78	78	78	142.35	26.8	03.4
30	L	00	43	65	70	70	70	70	70	70	113.75	28.0	01.8
	D	05	45	45	45	45	45	50	50	50	31.25	16.6	29.0
	L/D	05	53	60	63	63	63	63	65	65	114.83	30.4	04.8
35	L	00	00	00	23	43	53	55	55	55	41.64	02.3	01.7
	D	00	00	00	05	08	10	13	13	13	02.11	02.5	02.0
	L/D	00	00	43	53	55	58	58	58	58	61.48	06.0	03.1
20/10	L/D	00	00	00	00	25	55	78	80	80	78.00	02.1	01.4
25/15	L/D	00	00	18	38	65	73	75	75	75	78.21	16.3	02.1
30/20	L/D	00	18	53	58	68	68	68	70	70	97.33	20.8	03.9

App.(6.C): Saxifraga bronchialis

Temp. (C)	Light treat.	% germination after............days						GV	Root length (mm)	Shoot length (mm)
		5	6	7	8	9	10			
10		00	00	00	00	00	00	0.00	0.0	0.0
15		00	00	00	00	00	00	0.00	0.0	0.0
20	L	00	00	00	10	13	15	2.25	2.0	0.6
	D	00	00	00	00	00	00	0.00	0.0	0.0
	L/D	00	03	08	13	18	20	4.00	2.0	0.7
25	L	00	00	00	03	05	08	0.64	1.4	0.0
	D	00	00	00	00	00	00	0.00	0.0	0.0
	L/D	00	00	05	13	15	18	3.24	1.6	1.2
30		00	00	00	00	00	00	0.00	0.0	0.0
35		00	00	00	00	00	00	0.00	0.0	0.0
20/10	L/D	00	00	00	03	05	08	0.64	1.2	0.0
25/15	L/D	00	00	08	10	13	15	2.25	1.7	0.8
30/20	L/D	00	00	03	08	13	13	1.88	1.5	0.8

App.(6.D): Silene acaulis

Temp (C)	Light treat.	% germination after...........days							GV	Root length (mm)	Shoot length (mm)
		4	5	6	7	8	9	10			
10		00	00	00	00	00	00	00	0.00	00.0	00.0
15		00	00	00	00	00	00	00	0.00	00.0	00.0
20	L	00	00	00	00	00	00	00	0.00	00.0	00.0
	D	00	05	10	13	15	15	20	4.00	06.0	08.2
	L/D	00	03	03	03	05	08	08	0.71	13.0	02.5
25	L	00	00	00	00	00	00	00	0.00	00.0	00.0
	D	00	00	03	05	15	20	23	5.29	09.6	11.0
	L/D	00	00	00	05	08	08	08	0.80	05.4	02.0
30	L	00	00	05	08	08	08	08	0.91	02.1	03.7
	D	00	03	03	03	03	05	05	0.28	04.5	00.5
	L/D	00	03	05	08	08	10	10	1.11	03.5	01.0
35		00	00	00	00	00	00	00	0.00	00.0	00.0
20/10	L/D	00	00	00	00	03	05	05	0.28	01.6	00.5
25/15	L/D	00	00	03	05	05	08	10	1.00	02.4	00.5
30/20	L/D	00	00	00	05	08	13	18	3.24	07.0	02.0

App.(6.E): Dryas octopetala

Temp. (C)	Light treat.	% Germination after..............days 2	3	4	5	6	7	8	9	10	GV	Root length (mm)	Shoot length (mm)
10	L	00	00	00	00	00	00	00	00	00	00.00	00	00
	D	00	00	00	00	00	00	00	00	00	00.00	00.0	00.0
	L/D	00	00	00	00	00	03	05	05	05	00.31	03.1	00.0
15	L	00	00	00	00	00	03	05	05	05	00.31	03.8	02.5
	D	00	00	00	00	00	03	03	03	03	00.12	02.5	02.5
	L/D	00	00	00	00	03	03	05	05	05	00.31	04.2	03.0
20	L	00	00	05	08	08	08	08	08	08	01.28	04.7	01.0
	D	00	03	13	13	13	13	13	13	13	04.23	06.7	13.0
	L/D	00	05	05	08	08	08	08	08	08	01.28	09.3	02.8
25	L	03	05	08	08	08	08	08	08	08	01.26	18.6	03.0
	D	00	03	03	05	05	10	13	13	13	02.11	09.8	15.5
	L/D	00	03	08	08	10	10	10	10	10	01.67	16.0	04.0
30	L	00	05	08	13	13	15	15	18	18	03.60	08.0	02.6
	D	00	00	00	03	08	13	13	13	13	02.41	11.2	11.5
	L/D	03	13	20	23	28	28	30	33	33	12.10	10.8	02.0
35	L	00	00	00	03	03	05	05	05	05	00.36	02.8	01.8
	D	00	00	00	03	08	10	10	10	10	01.43	02.0	03.6
	L/D	00	00	05	08	08	08	08	08	08	01.60	01.5	02.0
20/10	L/D	00	00	00	03	03	08	08	08	08	00.91	01.8	00.0
25/15	L/D	00	00	00	05	08	08	08	10	10	01.11	09.2	02.3
30/20	L/D	00	03	05	08	13	15	20	23	23	05.68	12.5	02.6

Appendix (7): Effect of stratification on seed germination and seedling growth of the different species at constant temperature(24 C) day length=14 h . (n=100 seeds).
ERAN=Eriogonum androsaceum,POUN=Potentilla uniflora
SABR=Saxifraga bronchialis,SIAC=Silene acaulis,DROC=Dryas octopètala

Species	Stratif. time (days)	%germination after.........days 2	3	4	5	6	7	8	9	10	GV	Root length (mm)	Shoot length (mm)
ERAN	10	00	00	00	00	00	00	02	06	08	000.64	06.5	6.1
	20	00	00	00	00	00	00	02	02	04	000.16	04.5	4.2
	30	00	00	00	00	00	00	00	00	00	000.00	00.0	0.0
	40	00	00	00	00	00	00	00	00	00	000.00	00.0	0.0
	90	00	00	00	00	00	00	00	00	00	000.00	00.0	0.0
	control	00	00	00	00	00	00	02	04	04	000.16	05.6	6.2
POUN	10	28	86	94	94	94	94	94	94	94	220.90	28.3	2.5
	20	00	32	72	74	74	74	74	76	76	112.48	28.1	2.5
	30	00	18	40	52	58	68	70	76	76	073.83	26.5	2.2
	40	00	40	64	70	74	84	84	84	84	100.80	30.2	2.0
	90	00	06	44	54	64	64	70	72	72	063.00	04.1	1.8
	control	00	18	48	56	56	60	60	60	60	051.43	24.5	2.6
SABR	10	00	00	00	00	20	44	78	80	82	067.24	03.6	1.5
	20	00	00	00	02	06	14	24	40	46	021.16	03.2	1.0
	30	00	00	00	00	04	12	16	30	40	016.00	04.2	1.5
	40	00	00	00	02	06	14	20	26	32	010.24	01.5	1.3
	90	00	00	00	00	02	10	16	26	32	010.24	01.2	0.5
	control	00	00	00	00	02	04	08	13	18	003.24	01.4	1.2
SIAC	10	00	02	02	02	04	04	10	18	22	004.84	07.6	1.2
	20	02	06	08	08	12	14	18	22	26	006.76	20.5	2.4
	30	00	00	02	04	06	06	10	16	20	004.00	16.5	2.3
	40	02	02	04	06	08	08	08	16	18	003.24	15.6	2.4
	90	00	02	02	06	12	16	18	18	18	004.11	07.6	1.8
	control	00	00	03	03	05	08	10	10	13	001.63	05.4	2.5
DROC	10	00	04	04	06	08	08	10	12	12	001.44	16.1	4.3
	20	06	06	08	10	12	16	16	16	16	003.66	16.8	4.2
	30	00	04	08	08	08	12	16	16	16	003.20	10.5	4.1
	40	00	02	08	08	08	10	10	10	10	001.43	08.0	3.2
	90	00	00	02	02	02	04	04	04	04	000.23	04.5	2.0
	control	00	04	08	12	16	16	16	16	16	004.27	14.5	2.8

Appendix (8): Effect of washing and drying of seeds of the different species,at constant temperature(24C)and 14h day length.
W=washed seeds , NW=non-washed seeds. (n=5 with 50 seeds each).

Species	Treat.	%germination after.......days 3	4	5	6	7	8	9	10	GV	Root length (mm)	Shoot length (mm)
ERAN	W	00	00	00	00	04	12	16	16	00.84	07.4	6.8
	NW	00	00	00	00	05	05	07	07	00.54	06.5	6.2
POUN	W	32	65	67	69	70	74	80	80	71.11	30.2	3.5
	NW	30	55	68	74	74	76	76	76	72.20	26.8	3.4
SABR	W	00	00	00	00	04	12	28	40	16.00	01.8	1.5
	NW	00	00	00	00	02	12	16	20	04.00	01.6	1.5
SIAC	W	00	00	00	08	20	24	28	36	12.96	05.5	2.1
	NW	00	00	00	00	04	08	10	12	01.44	05.4	2.0
DROC	W	08	12	20	20	32	32	32	32	14.63	17.6	3.8
	NW	04	06	09	10	10	13	13	13	02.11	16.5	3.6

Appendix (9): Effect of water availability on seed germination and seedling growth of some of the species investigated. (n=100 seeds).

App.(9.A): Effect of mannitol and sodium chloride (osmotic pressure) on seed germination and seedling growth of Potentilla uniflora(POUN) and Silene acaulis(SIAC) at constant temperature(24C).14h day length

Species	Osmotic pressure (atm.)	% germination after.........days									GV	Root length (mm)	Shoot length (mm)
		2	3	4	5	6	7	8	9	10			
POUN	Mannitol												
	1	00	04	48	72	74	74	74	76	76	80.34	13.2	3.5
	3	00	00	22	68	72	74	74	74	74	78.23	03.5	1.8
	5	00	00	06	08	38	44	50	52	52	32.50	03.2	1.5
	7	00	00	02	10	36	38	44	45	45	24.75	02.9	1.5
	10	00	00	00	02	16	24	36	38	38	17.10	02.5	1.5
	Sodium chloride												
	1	00	00	16	52	66	66	66	66	66	72.60	10.5	1.8
	3	00	00	12	52	58	64	66	66	66	60.34	09.0	1.5
	5	00	00	12	30	52	54	64	64	64	51.20	02.0	1.0
	7	00	00	05	28	46	52	58	58	58	42.05	01.2	1.0
	10	00	00	00	04	32	48	54	54	54	36.45	00.8	0.8
	Control	00	10	50	72	76	80	80	80	80	91.43	21.5	2.0
SIAC	Mannitol												
	1	00	00	00	00	00	02	04	04	06	00.36	01.5	0.5
	3	00	00	00	00	00	00	02	02	04	00.16	01.5	0.0
	5	00	00	00	00	00	00	00	00	00	00.00	00.0	0.0
	Sodium chloride												
	1	00	00	00	02	04	04	06	06	08	00.64	02.0	1.5
	3	00	00	00	00	02	03	04	06	06	00.40	01.8	1.2
	5	00	00	00	00	02	02	03	03	03	00.11	01.5	0.5
	7	00	00	00	00	00	00	00	02	03	00.09	00.5	0.0
	10	00	00	00	00	00	00	00	00	00	00.00	00.0	0.0
	Control	00	00	00	04	04	06	06	08	12	01.44	10.2	2.0

App.(9.B): Effect of substrate water content (log scale) on seed germination and seedling growth of Potentilla uniflora (POUN) and Silene acaulis (SIAC) at constant temperature (24C) and 14h day length .

Species	Substrate water cont*	%germination after.....days					GV	Root length (mm)	Shoot length (mm)
		2	4	6	8	10			
POUN	2.4	00	76	84	84	84	117.60	17.5	2.0
	2.5	00	70	88	92	92	118.29	15.3	2.0
	2.6	00	84	90	96	96	127.54	15.5	2.2
	2.7	00	76	80	80	80	124.80	20.3	2.4
	2.8	00	66	72	76	76	091.20	16.8	2.3
	2.9	00	66	70	70	70	081.67	12.5	2.1
SIAC	2.4	00	00	03	04	04	000.20	02.2	0.8
	2.5	00	00	03	05	06	000.36	06.5	2.5
	2.6	00	00	04	06	08	000.64	07.8	2.5
	2.7	00	00	08	08	10	001.00	08.1	1.9
	2.8	00	02	06	08	11	001.21	06.5	2.2
	2.9	00	06	08	12	14	001.96	07.8	1.5

* based on dry wt of the filter paper substrate

Appendix (10): Germination and seedling growth of various species under different treatments of some growth regulators at 24 c Day length 14 hr . GV=germination value. (n=100 seeds)

App (10.A) Eriogonum androsaceum

Treatment (-log molar)		%germination after..........days 3	4	5	6	7	8	9	10	GV	Root length (mm)	Shoot length (mm)
Thiourea	3.3	00	00	00	00	02	05	06	06	0.40	02.8	3.6
	2.3	00	00	00	00	00	04	04	06	0.36	02.5	3.1
	2.0	00	00	00	00	00	02	02	04	0.16	01.8	2.5
	1.7	00	00	00	00	00	00	00	00	0.00	00.0	0.0
Pot.nitr.	3.3	00	00	03	05	08	10	10	17	2.89	16.2	15.5
	2.3	00	00	02	03	08	09	10	13	1.69	10.2	10.0
	2.0	00	00	00	00	03	03	05	10	1.00	10.8	05.1
	1.7	00	00	03	05	06	10	10	10	1.25	10.5	04.6
	1.5	00	00	00	00	04	05	08	08	0.71	05.5	03.5
	1.4	00	00	00	00	02	04	07	08	0.64	04.1	03.2
	1.3	00	00	00	00	00	00	02	05	0.25	02.5	01.5
GA3	5.3	00	00	02	03	05	05	07	08	0.49	02.6	04.8
	4.3	00	02	02	02	03	04	08	10	0.64	02.5	04.2
	3.3	00	00	03	03	05	10	13	20	4.00	02.2	03.8
	2.3	00	00	03	08	17	17	20	25	6.25	03.5	03.6
	2.0	00	05	05	08	13	18	22	27	7.29	03.3	06.1
	1.7	00	00	03	09	09	10	18	22	4.84	03.0	05.8
Kinetin	5.3	00	00	00	00	02	03	05	05	0.25	04.5	06.3
	4.3	00	00	03	03	04	05	08	13	1.69	04.6	04.9
	3.3	00	02	08	08	08	10	10	15	2.25	05.2	09.0
	2.3	00	00	03	08	17	18	20	22	4.84	04.2	09.5
	2.0	00	02	03	07	10	10	15	15	2.50	05.5	08.4
	1.7	00	00	04	05	05	12	13	13	1.88	03.5	05.7
Control		00	00	00	02	03	04	04	06	0.36	10.5	10.3

App.(10.B): Potentilla uniflora

Treatment (-log molar)		%germination after..........days 2	3	4	5	6	7	8	9	10	GV	Root length (mm)	Shoot length (mm)
Thiourea	3.3	00	42	52	60	60	60	62	62	62	048.05	27.2	03.1
	2.3	34	54	58	60	62	62	62	62	62	064.07	16.5	02.4
	2.0	22	82	84	84	86	88	88	88	88	110.63	03.4	02.3
	1.7	16	80	82	82	84	86	86	86	86	105.66	02.6	01.9
	1.5	14	72	74	74	74	74	74	74	74	136.90	01.9	01.8
	1.4	12	60	62	64	64	68	70	70	70	061.25	01.2	01.7
	1.3	08	56	56	58	62	64	66	66	66	054.45	01.1	01.5
Pot.nitr.	3.3	00	68	75	88	91	91	91	91	91	138.02	21.5	02.5
	2.3	00	58	70	70	83	85	85	88	88	086.04	24.5	02.5
	2.0	00	63	88	88	91	91	91	91	91	138.02	26.0	02.6
	1.7	00	48	83	83	83	83	88	88	88	096.80	22.3	02.2
	1.5	00	23	83	85	88	91	91	91	91	118.30	17.5	02.3
	1.4	00	23	88	91	91	91	91	91	91	165.62	13.6	02.7
	1.3	00	18	73	78	78	78	80	80	80	080.00	08.2	02.5
GA3	5.3	00	63	75	83	85	85	85	85	85	120.42	06.1	13.7
	4.3	00	70	85	85	88	88	88	88	88	129.07	05.8	13.5
	3.3	00	50	73	75	75	75	75	75	75	112.50	02.3	10.1
	2.3	00	20	35	45	48	50	50	50	50	035.71	01.0	01.5
	2.0	00	00	05	13	25	25	25	25	25	010.42	00.5	00.8
	1.7	00	00	00	05	08	08	08	08	08	001.07	00.5	00.6
Kinetin	5.3	00	30	60	63	68	68	68	68	68	077.07	07.1	02.5
	4.3	00	33	63	65	68	70	70	70	70	070.00	07.5	02.4
	3.3	00	23	68	70	70	70	70	70	70	098.00	07.5	02.8
	2.3	00	15	63	65	65	70	70	70	70	070.00	07.8	02.5
	2.0	00	20	60	65	68	68	68	68	68	077.07	06.5	03.1
	1.7	00	13	45	50	58	58	58	58	58	056.07	06.1	03.0
Control		00	52	60	64	66	66	66	66	66	072.60	28.1	02.5

App (10.C): Saxifraga bronchialis

Treatment (-log molar)		%germination after .... days							GV	Root length (cm)	Shoot length (cm)
		4	5	6	7	8	9	10			
Thiourea	3.3	00	00	00	06	06	14	20	04.00	1.7	1.7
	2.3	00	00	00	04	04	10	14	01.96	1.2	0.5
	2.0	00	00	00	00	02	04	05	00.25	0.5	0.0
	1.7	00	00	00	00	00	00	00	00.00	0.0	0.0
Pot.nitr.	3.3	00	00	00	03	13	13	15	02.25	1.2	0.8
	2.3	00	00	02	03	05	13	18	03.24	1.5	1.5
	2.0	00	00	03	08	15	23	28	07.84	1.8	1.5
	1.7	00	00	00	03	13	20	25	06.25	1.0	1.0
	1.5	00	00	00	08	10	20	23	05.29	0.8	0.6
	1.4	00	00	00	05	13	18	20	04.00	0.8	0.8
	1.3	00	00	00	00	10	16	16	02.56	0.7	0.7
GA3	5.3	00	10	36	60	76	80	80	64.00	1.9	2.8
	4.3	00	08	30	58	70	72	78	60.84	1.8	2.5
	3.3	00	02	20	48	56	60	66	43.56	1.0	0.5
	2.3	00	00	06	10	12	12	14	01.96	0.5	0.0
	2.0	00	00	00	00	00	05	08	00.64	0.5	0.0
	1.7	00	00	00	00	00	00	00	00.00	0.0	0.0
Kinetin	5.3	00	00	00	05	12	17	28	07.84	1.5	1.5
	4.3	00	00	04	15	20	30	40	16.00	1.8	1.6
	3.3	00	00	03	10	18	35	49	24.01	2.5	2.0
	2.3	00	00	00	12	25	32	40	16.00	2.3	2.0
	2.0	00	00	00	10	12	18	28	07.84	1.5	1.8
	1.7	00	00	02	08	10	10	10	01.25	0.5	0.8
Control		00	00	00	04	05	10	16	02.56	2.4	1.5

App.(10.D): Silene acaulis

Treatment (-log molar)		%germination after .... days									GV	Root length (mm)	Shoot length (mm)
		2	3	4	5	6	7	8	9	10			
Thiourea	3.3	00	00	00	00	00	04	04	06	06	00.40	05.3	1.4
	2.3	00	00	00	00	00	02	06	08	08	00.71	02.5	1.6
	2.0	00	02	04	04	04	06	06	08	08	00.71	01.9	1.5
	1.7	00	02	02	02	04	04	04	06	06	00.40	01.7	0.8
	1.5	00	00	00	00	00	00	00	00	00	00.00	00.0	0.0
Pot.nitr:	3.3	00	00	00	00	03	03	05	05	05	00.31	03.5	1.2
	2.3	00	00	00	00	00	00	03	08	08	00.71	03.5	1.2
	2.0	00	00	00	00	03	05	05	05	08	00.64	03.2	1.4
	1.7	00	00	00	00	03	03	03	05	10	01.00	03.2	1.5
	1.5	00	00	00	00	03	05	08	10	13	01.69	03.0	1.5
	1.4	00	00	00	00	03	03	08	13	13	01.88	03.0	1.5
	1.3	00	00	00	00	00	03	03	05	08	00.64	01.5	1.5
GA3	5.3	00	10	30	38	58	68	83	83	92	84.64	10.5	4.8
	4.3	00	08	25	40	48	55	70	85	88	77.44	09.5	4.5
	3.3	00	03	10	15	18	20	20	33	35	12.25	02.0	3.5
	2.3	00	10	10	15	20	20	20	28	28	08.71	01.0	1.5
	2.0	00	05	08	08	13	13	18	20	20	04.44	00.8	0.8
	1.7	00	00	00	03	03	05	08	08	08	00.80	00.5	0.5
Kinetin	5.3	00	03	03	08	08	08	10	10	10	01.25	19.5	3.3
	4.3	00	05	05	05	05	10	13	15	15	02.50	19.5	3.0
	3.3	00	03	08	13	13	15	15	18	18	03.60	19.0	2.5
	2.3	00	00	05	13	18	18	18	20	20	04.44	17.5	3.0
	2.0	00	00	00	00	08	10	20	23	25	06.25	12.0	3.5
	1.7	00	00	00	00	03	08	08	13	13	01.88	08.5	3.0
Control		00	02	04	04	06	10	16	18	18	03.60	05.2	2.3

App.(10.E):-Dryas octopetala

Treatment (-log molar)		%germination after..........days									GV	Root length (mm)	Shoot length (mm)
		2	3	4	5	6	7	8	9	10			
Thiourea	3.3	00	03	03	03	05	05	08	08	08	0.80	11.2	2.3
	2.3	00	03	05	05	08	08	10	10	10	1.25	12.2	3.5
	2.0	00	00	03	03	05	05	05	05	05	0.42	05.1	2.6
	1.7	00	00	03	03	03	05	05	05	05	0.36	03.4	0.5
	1.5	00	00	03	05	05	05	05	05	05	0.50	03.2	0.0
	1.4	00	00	02	02	02	03	03	03	03	0.13	03.0	0.0
	1.3	00	00	00	00	02	02	02	02	02	0.07	03.0	0.0
Pot.nitr.	3.3	00	00	03	03	04	05	05	05	05	0.36	06.0	2.5
	2.3	00	00	00	02	05	05	08	08	08	0.80	05.5	2.5
	2.0	00	00	00	05	05	08	13	13	13	2.11	04.0	2.0
	1.7	00	05	05	10	13	13	15	15	15	2.81	05.1	3.9
	1.5	00	00	05	05	08	08	13	15	15	2.50	04.3	2.2
	1.4	00	00	02	05	10	10	10	10	10	1.67	03.6	2.4
	1.3	00	00	02	02	03	08	10	12	12	1.60	02.5	2.5
GA3	5.3	00	00	04	04	10	10	10	10	10	1.67	02.2	3.5
	4.3	00	00	03	04	07	07	07	07	07	1.17	01.8	3.2
	3.3	00	00	02	02	02	03	04	04	04	0.80	02.0	4.1
	2.3	00	00	00	00	00	00	00	00	00	0.00	00.0	0.0
Kinetin	5.3	00	00	04	04	07	07	07	07	07	1.17	06.7	3.0
	4.3	00	00	00	03	04	07	07	07	07	0.70	06.5	2.8
	3.3	00	00	07	10	13	13	13	13	13	2.82	05.7	2.5
	2.3	00	00	00	06	07	10	10	10	10	1.43	04.5	2.3
	2.0	00	00	00	10	13	13	16	15	16	3.20	04.2	2.0
	1.7	00	00	00	04	08	13	13	13	13	2.82	03.6	1.8
Control		00	05	05	08	08	08	10	10	10	1.25	07.4	2.8

Appendix (11): Effect of chilling and dehydration on seedling Survival and establishment (%) . POUN=Potentilla uniflora, SIAC=Silene acaulis, and SABR=Saxifraga bronchialis. (n=50 seedlings per species every treatment period).

Species	Treatm.	Treatment period......................hours						
		3	6	9	12	18	24	48
POUN	Chilling	100	98	94	92	86	80	35
	Dehydration	98	96	92	88	70	46	08
SIAC	Chilling	100	94	92	86	80	62	24
	Dehydration	90	86	70	62	28	16	00
SABR	Chilling	96	88	76	72	62	51	13
	Dehydration	96	80	63	45	19	04	00

Appendix (12): Effect of leaf temperature (C) on net photosynthesis at 460 umol/m2/sec.,and dark respiration of the different species. Each value represents the average of three measurements.

App.(12.A): Eriogonum androsaceum.

Leaf temperature (C)	net photosynthesis mg co2.g DW.h	net photosynthesis mg co2.dm.h	dark respiration mg co2.g DW.h	dark respiration mg co2.dm.h
1.5	-1.52	-03.26		
5.0	1.54	03.30		
5.5			-07.33	-15.70
8.0			-11.40	-24.40
8.5	2.44	05.20		
10.5	3.72	08.00		
12.0			-15.06	-32.20
13	5.70	12.20		
17.0	9.36	20.00		
19.0			-16.28	-34.80
19.5	9.36	20.00		
20.0	7.75	16.80		
21.0	9.77	20.90		
27.0	7.33	15.70		
30.0	3.67	07.90	-17.09	-36.50
33.0	0.81	01.70		
35.5	0.81	01.70		

App.(12.B): Potentilla uniflora.

Leaf temperature (C)	net photosynthesis mg co2.g DW.h	net photosynthesis mg co2.dm.h	dark respiration mg co2.g DW.h	dark respiration mg co2.dm.h
1	-1.80	-03.28		
3	1.69	03.06		
4			-0.60	-1.00
5			-0.60	-1.00
6			-0.78	-1.70
6.5			-1.49	-2.70
7			-0.78	-1.70
7.5	1.49	02.70		
8			-1.79	-3.20
8.5	0.86	02.00		
9			-0.86	-2.00
10	2.12	04.40	-0.86	-2.00
11			-0.90	-1.50
13			-0.78	-1.70
14	3.45	08.00	-1.29	-3.00
15.5	4.77	08.60		
17	5.94	12.00		
17.5	6.13	13.00	-0.90	-1.50
18	6.18	13.10	-1.78	-4.30
18.5	5.03	11.60		
19	8.45	17.40		
19.5	8.64	16.60		
20	8.36	14.75		
21			-1.87	-4.30
21.5	9.24	16.70		
22	7.98	16.90		
23	5.68	12.30	-2.16	-5.00
23.5	7.03	14.90		
24	6.96	14.70	-3.28	-5.90
25	6.75	15.60		
25.5	4.78	10.20		
28.5			-2.59	-6.00
29	3.74	06.60		
30			-2.38	-4.30
31			-3.59	-8.30
31.5	1.51	03.50		
33	0.78	01.70	-4.17	-7.50
34			-4.77	-8.60
37	0.89	01.60		

App.(12.C): Saxifraga caespitosa.

Leaf temperature (C)	net photosynthesis		dark respiration	
	mg co2.g DW.h	mg co2 dm.h	mg co2.g DW.h	mg co2.dm.h
2	00.00	00.00		
3	00.25	00.40	-0.25	-0.40
3.5	01.02	00.90		
4	01.04	00.70	-0.30	-0.40
5			-0.50	-0.70
5.5	01.63	02.30	-0.30	-0.30
6	02.30	02.85	-0.15	-0.20
6.5	03.70	05.33		
7	03.70	03.75		
7.5	03.60	03.93		
8	04.00	04.90		
9			-0.50	-0.70
9.5			-0.45	-0.40
10			-0.30	-0.4
10.5	05.38	07.70		
11	05.64	05.85		
13	07.25	06.50		
13.5	06.00	08.60		
14	05.48	06.70		
14.5			-1.60	-1.40
15.5			-2.52	-3.10
16			-2.47	-2.20
16.5	05.08	04.60		
17	06.45	08.65	-2.96	-3.60
17.5			-2.90	-2.60
18	06.29	08.45	-2.00	-2.90
18.5	07.00	10.10		
19	08.41	07.50	-2.90	-2.60
19.5	07.13	10.30	-2.25	-3.20
20	08.12	07.30		
20.5	05.03	06.10		
21	06.63	09.50		
22	06.13	08.80	-3.34	-3.00
22.5			-2.25	-3.2
23	05.22	04.70		
23.5	06.50	09.40		
25			-4.06	-3.60
25.5			-3.25	-4.70
27	05.77	07.00		
28			-3.40	-4.10
28.5			-4.64	-4.20
29	04.35	03.90		
29.5			-2.88	-4.10
30	06.13	08.80		
30.5	04.14	05.00	-3.48	-3.10
32	03.55	04.30	-2.13	-3.10
34	03.57	04.40		
35	03.88	05.60		

App.(12.D): Saxifraga bronchialis.

Leaf temperature (C)	net photosynthesis		dark respiration	
	mg co2.g DW.h	mg co2.dm.h	mg co2.g DW.h	mg co2.dm.h
3	-1.77	-1.99		
4	0.62	0.70	-0.10	-0.10
4.5	-0.59	0.50		
5	1.48	1.30		
5.5	1.63	1.40	-0.30	-0.30
6	1.96	2.27	-0.21	-0.20
6.5	2.97	3.00		
7	3.30	3.80		
8.5			-0.59	-0.50
9.5			-0.72	-0.80
10.5	3.50	4.10		
11	3.40	3.00		
12.5	4.00	3.50		
13	3.61	4.20	-1.48	-1.30
14			-1.03	-1.20
15.5			-1.24	-1.40
16	3.92	3.90	-1.48	-1.30
16.5	3.81	4.45		
17	4.02	4.70	-1.65	-1.60
17.5	4.43	5.20	-2.66	-2.30
18	5.03	4.40		
18.5	4.63	4.65		
19			-2.06	-2.40
19.5	4.00	3.50		
20	4.33	5.00	-2.96	-2.60
21	4.02	4.70		
21.5	5.77	5.10		
22	4.53	5.30	-4.59	-4.00
22.5			-3.19	-3.70
24.5			-4.12	-5.10
25.5	5.46	6.40	-5.92	-5.20
27	6.66	5.90		
27.5	4.14	3.60		
28	3.71	4.30	-2.68	-3.10
28.5			-3.26	-2.90
30.5			-2.06	-2.40
31	2.81	2.50		
31.5			-2.66	-2.30
32.5	2.99	3.50		
33.5	2.37	2.10		
34	2.16	2.50		

App.(12.E): Silene acaulis

Leaf temperature (C)	net photosynthesis		dark respiration	
	mg Co2.g DW.h)	mg Co2.dm.h)	mg Co2.g DW.h)	mg Co2.dm.h)
2	-01.00	-01.35		
5			-2.30	-3.20
6			-2.92	-3.80
7	02.45	03.30		
7.5	01.35	01.90	-2.70	-3.80
8			-4.16	-5.20
8.5			-3.74	-4.70
9	04.42	06.90	-3.11	-4.40
9.5	03.38	04.80		
10	03.74	04.70		
11			-3.25	-4.80
12			-3.74	-4.70
13	08.32	11.20	-3.52	-4.65
14	05.40	07.60		
14.5	06.66	08.30		
16	09.05	12.20	-3.65	-5.10
16.5	05.54	07.80		
17.5	06.86	08.60	-4.78	-6.00
19	10.03	13.50		
20.5	10.15	13.80	-4.91	-6.45
21	06.08	08.60		
22	09.78	15.20		
22.5			-4.53	-5.95
24	09.15	11.40		
24.5	11.50	15.50		
26	09.98	12.50	-3.12	-3.90
27	07.16	10.10		
28	10.19	15.10		
28.5			-5.62	-7.00
29			-5.40	-7.60
30	06.86	08.60		
30.5	04.73	06.70	-6.24	-7.80
31	04.80	08.20	-4.16	-5.20
32			-5.54	-7.80
32.5	03.12	03.90		
33	02.30	03.20		
34	01.46	01.80		
34.5	01.21	01.70		
35	01.63	01.65		

App.(12.F): Dryas octopetala.

Leaf temperature (C)	Net photosynthesis		dark respiration	
	mg Co2.g DW.h	mg Co2.dm.h	mg Co2.g DW.h	mg Co2.dm.h
2.5			-0.09	-0.20
3	-1.58	-03.56		
3.5			-0.19	-0.40
4.5			-0.80	-0.40
5.5	0.40	00.90	-0.19	-0.40
6	0.53	01.00		
7	1.34	02.70	-0.40	-0.90
7.5	2.27	04.80		
8			-0.56	-1.30
9.5	3.46	07.30		
10			-0.66	-1.50
10.5			-0.56	-1.30
11	2.78	06.00		
12	4.39	09.40		
16			-0.74	-1.70
16.5	3.45	08.00		
17.5	5.27	11.90	-1.46	-3.00
18	7.41	16.80	-1.45	-3.30
18.5	4.24	10.00		
19	7.16	17.00	-0.93	-2.10
19.5			-1.99	-4.50
20	7.15	16.00	-2.21	-5.00
21	4.98	11.00		
21.5	7.16	17.00		
22	8.11	19.00		
23.5	8.02	18.30		
24.5			-2.12	-2.70
25	7.96	18.10		
25.5	6.40	13.00		
26.5			-1.12	-2.50
27	8.59	15.40		
27.5	5.69	13.00		
28.5	6.09	13.70		
29	4.81	19.00	-0.74	-1.70
29.5	4.41	09.90		
30.5			-0.93	-2.00
31			-1.99	-4.50
35			-1.59	-3.60

Appendix (13): Effect of light intensity on net photosynthesis of the different species at constant air temperature (22.7+-1.6 C). Each value represents the average of three measurements.

App.(13.A): Eriogonum androsaceum.

Light intensity (mol m.sec)	net photosynthesis	
	mg co2.g DW.h	mg co2.dm.h
15	-19.15	-40.71
20	-18.92	-40.81
105	-16.30	-34.64
118	-03.41	-07.36
135	-06.20	-13.38
150	-08.96	-19.05
155	-04.34	-07.40
180	-01.86	-04.01
230	-02.44	-05.20
250	-04.88	-13.00
350	03.67	07.79
420	12.71	19.43
610	02.04	04.33
675	01.63	03.46

App.(13.B): Potentilla uniflora.

Light intensity (mol m.sec)	net photosynthesis	
	mg co2.g DW.h	mg co2.dm.h
15	-8.05	-15.90
105	-1.49	-02.95
110	-1.36	-03.80
150	1.51	03.05
160	1.26	02.50
180	3.32	03.00
230	3.61	07.22
250	3.34	06.60
450	7.31	12.50
610	7.70	15.20
675	9.76	19.30

App.(13.C): Saxifraga caespitosa.

Light intensity (mol m.sec)	net photosynthesis	
	mg co2.g DW.h	mg co2.dm.h
15	-07.07	-08.00
20	-08.23	-09.40
105	04.50	05.10
110	05.78	06.60
118	07.22	08.20
135	08.23	09.40
155	09.64	11.00
180	14.56	16.50
230	14.13	16.10
250	20.56	23.40
450	19.84	22.60
610	14.78	16.80
675	14.13	16.10

App.(13.D): Saxifraga bronchialis

Light intensity (mol m.sec)	net photosynthesis mg co2.g DW.h	mg co2.dm.h
15	-05.58	-05.60
105	02.87	02.90
110	04.07	04.10
155	02.93	03.00
160	05.73	05.80
180	04.83	04.90
230	07.24	07.30
250	10.41	10.50
450	07.82	07.90
610	06.49	06.60
675	09.20	09.30

App.(13.E): Silene acaulis.

Light intensity (mol m.sec)	net photosynthesis mg Co2.g Dw.h	mg Co2.dm.h
105	-03.44	----
110	-02.78	----
160	-02.15	----
180	02.74	----
230	05.65	----
250	05.89	----
450	08.50	----
610	09.52	----
675	11.66	----

App.(13.F): Dryas octopetala.

Light intensity (mol m sec)	net photosynthesis mg Co2.g DW.h	mg Co2.dm.h
15	-3.81	-08.58
105	3.50	07.89
110	3.50	07.89
150	3.96	08.92
160	5.71	12.86
180	6.31	14.23
230	7.61	17.15
250	8.14	18.35
450	9.00	18.12
610	9.21	20.75
675	5.20	11.73

Appendix (14): the water content(%fresh wt),transpiration rate(mg/g fresh wt),water saturation deficit(%),and water potential(bar)of transpiring organs of the studied species at different controlled air temperatures(C)and water treatments(W=watered plants,NW=non-watered plants). Radiation intensity=650 uE,Wind velocity=30 feet/min, and Relative humidity=50/60%.Standared deviations in brackets.

App.(14.A): Eriogonum androsaceum.(n=4).

Temp.	Treat.	Water cont.	Transpiration	WSD	Water potential
05	W	80(1.06)	99(01.34)	21(1.05)	14(0.35)
	NW	75(0.42)	68(03.18)	23(0.35)	16(0.35)
10	W	77(0.99)	238(10.11)	24(0.45)	16(0.46)
	NW	73(0.92)	116(06.65)	25(0.95)	18(0.00)
15	W	76(1.06)	621(14.64)	26(0.25)	21(0.71)
	NW	72(1.13)	294(16.62)	27(0.00)	25(0.35)
20	W	76(0.35)	704(18.24)	27(0.50)	27(0.71)
	NW	69(1.77)	427(23.48)	29(1.25)	28(0.35)
25	W	75(0.78)	731(15.34)	31(1.05)	29(0.71)
	NW	66(0.57)	502(08.42)	33(0.45)	30(0.35)
30	W	69(1.06)	724(16.05)	35(1.45)	30(0.71)
	NW	65(1.20)	296(12.94)	36(0.85)	32(0.71)
Average	W	76(3.30)	520(235.95)	28(4.35)	23(6.26)
	NW	70(3.65)	284(154.43)	29(4.49)	25(5.96)
Range	W	69-80	99-731	22-35	14-30
	NW	65-75	68-502	23-36	16-32
Ratio	W/NW	1.09	1.83	-	-
	NW/W	-	-	1.04	1.10

App.(14.B): Potentilla uniflora. (n=5).

Temp	Treat	Water cont	Transpiration	WSD	Water potential
5	W	75(2.12)	336(30.07)	54(0.76)	12(0.41)
	NW	69(1.50)	152(48.22)	56(0.54)	16(0.48)
10	W	74(1.61)	413(17.78)	56(1.00)	14(0.87)
	NW	65(0.79)	161(24.42)	58(0.53)	16(0.48)
15	W	70(0.75)	504(21.71)	59(1.20)	15(0.65)
	NW	64(1.53)	237(20.85)	63(2.02)	17(0.65)
20	W	69(1.20)	555(31.47)	61(1.21)	16(0.41)
	NW	63(0.83)	290(29.74)	65(1.28)	19(0.65)
25	W	67(3.15)	558(25.02)	63(1.03)	18(0.41)
	NW	62(1.35)	367(44.16)	65(2.23)	20(0.41)
30	W	59(1.41)	687(37.97)	64(2.48)	18(1.08)
	NW	49(1.68)	305(14.51)	66(1.00)	26(2.02)
Average	W	69(5.26)	509(112.08)	60(3.59)	16(2.14)
	NW	62(6.22)	252(077.14)	62(3.80)	19(3.46)
Range	W	59-75	336-687	54-64	12-18
	NW	49-69	152-367	56-66	16-26
Ratio	W/NW	1.11	2.02	-	-
	NW/W	-	-	1.03	1.19

App.(14.C): Saxifraga caespitosa. (n=4).

Temp	Treat	Water cont	Transpiration	WSD	Water potential
5	W	84(0.99)	029(03.83)	17(0.68)	09(0.63)
	NW	81(1.48)	016(05.06)	27(0.89)	11(0.25)
10	W	83(0.88)	041(05.21)	24(0.58)	10(0.29)
	NW	81(0.72)	034(04.34)	28(0.37)	11(0.40)
15	W	83(0.74)	098(20.19)	24(0.72)	10(0.41)
	NW	80(0.62)	049(03.67)	29(0.58)	12(0.48)
20	W	82(1.48)	131(03.66)	26(0.47)	12(1.08)
	NW	79(1.45)	051(11.81)	29(0.80)	17(0.48)
25	W	82(0.51)	166(21.07)	27(0.45)	16(1.08)
	NW	78(0.41)	094(21.65)	32(0.69)	19(1.08)
30	W	77(0.65)	114(33.81)	27(0.62)	18(0.25)
	NW	74(0.47)	040(03.79)	33(2.23)	22(1.03)
Average	W	82(2.10)	097(48.25)	24(3.44)	13(3.35)
	NW	79(2.41)	047(23.83)	30(2.13)	15(4.27)
Range	W	77-84	26-166	12-27	9-13
	NW	74-81	16- 94	27-33	11-22
Ratio	W/NW	1.04	2.06	-	-
	NW/W	-	-	1.25	1.15

App.(14.D): Saxifraga bronchialis

Temp	Treat	Water cont	Transpiration	WSD	Water potential
5	W	83(1.16)	047(11.16)	09(0.68)	05(0.63)
	NW	76(0.68)	022(05.96)	14(0.51)	06(0.41)
10	W	84(1.86)	114(06.04)	12(0.47)	06(0.25)
	NW	78(0.83)	059(22.51)	14(0.94)	08(1.19)
15	W	82(2.91)	164(07.13)	15(0.63)	06(0.85)
	NW	76(0.13)	112(17.16)	17(0.46)	09(0.41)
20	W	82(0.91)	347(15.39)	17(0.78)	09(0.25)
	NW	75(1.79)	117(16.58)	20(2.58)	10(0.25)
25	W	80(0.58)	296(55.31)	19(2.63)	09(0.91)
	NW	75(1.15)	058(28.87)	28(1.14)	12(0.48)
30	W	67(1.98)	219(44.18)	42(1.41)	11(0.63)
	NW	61(1.78)	054(09.09)	53(2.18)	14(0.29)
Average	W	80(5.79)	198(102.68)	19(10.79)	08(2.13)
	NW	74(5.68)	070(033.66)	24(13.67)	10(2.61)
Range	W	67-84	47-347	9-42	5-11
	NW	61-78	22-117	14-53	6-14
Ratio	W/NW	1.08	2.54	-	-
	NW/W	-	-	1.26	1.25

App.(14.E): Silene acaulis.(n=5).

Temp	Treat	Water cont	Transpiration	WSD	Water potential
5	W	86(0.95)	079(07.15)	14(0.42)	07(0.25)
	NW	85(0.44)	046(20.89)	16(0.50)	08(0.41)
10	W	88(0.95)	099(15.54)	16(0.42)	10(0.65)
	NW	84(0.45)	052(05.29)	18(0.56)	13(0.25)
15	W	85(0.50)	251(33.38)	16(0.79)	11(0.41)
	NW	80(1.88)	180(09.69)	20(0.86)	14(0.65)
20	W	83(0.25)	409(59.33)	17(0.30)	12(0.48)
	NW	80(0.83)	265(36.40)	19(0.62)	15(1.97)
25	W	82(0.41)	477(56.48)	19(0.38)	13(0.25)
	NW	81(0.25)	289(44.76)	20(0.26)	16(0.48)
30	W	77(3.34)	399(43.81)	22(0.74)	13(0.85)
	NW	72(2.21)	268(26.95)	23(0.65)	16(1.55)
Average	W	84(3.50)	286(154.61)	17(2.56)	11(2.08)
	NW	80(4.19)	183(100.93)	19(2.13)	14(2.75)
Range	W	77-88	79-477	14-22	7-13
	NW	72-85	46-289	16-23	8-16
Ratio	W/NW	1.05	1.56	-	-
	NW/w	-	-	1.12	1.27

App.(14.F): Dryas octopetala. (n=5).

Temp	Treat	Water cont	Transpiration	WSD	Water potential
5	W	69(4.43)	020(00.84)	34(0.97)	07(0.85)
	NW	52(2.33)	015(00.70)	38(1.05)	09(0.64)
10	W	65(5.70)	128(16.13)	34(1.38)	09(0.48)
	NW	51(2.49)	048(13.51)	39(1.08)	11(0.91)
15	W	61(2.92)	174(25.02)	40(0.75)	10(1.38)
	NW	51(1.21)	072(14.04)	42(1.01)	14(1.55)
20	W	56(1.78)	275(44.11)	40(0.87)	12(1.25)
	NW	51(1.79)	113(32.98)	44(1.86)	15(1.04)
25	W	54(3.16)	371(36.64)	41(1.48)	13(1.00)
	NW	50(1.52)	182(39.30)	45(0.56)	16(0.91)
30	W	47(2.56)	567(61.78)	43(1.35)	13(1.64)
	NW	42(2.66)	188(59.84)	45(1.28)	21(1.25)
Average	W	59(7.27)	256(177.53)	39(3.45)	11(2.21)
	NW	50(3.40)	103(064.93)	42(2.79)	14(3.82)
Range	W	47-69	20-567	34-43	7-13
	NW	42-52	15-188	38-45	9-21
Ratio	W/NW	1.18	2.49	-	-
	NW/W	-	-	1.08	1.27

Appendix (15): Variation of Cushion-plant leaf temperature under controlled environment. W=watered plants NW=nonwatered plants .

Species	Treat.	Air temperature(C) and relative humid					
		5 RH=83	10 RH=80	15 RH=75	20 RH=55	25 RH=45	30 RH=35
Eriogonum androsaceum	W	7.4	11.2	13.8	22.1	26.2	29.6
	NW	7.9	11.2	15.7	22.6	26.4	30.8
Potentilla uniflora	W	8.6	13.3	15.7	24.0	26.4	30.4
	NW	7.8	11.3	15.5	22.6	26.7	31.3
Saxifraga caespitosa	W	8.3	13.0	15.6	22.8	27.5	30.2
	NW	8.0	13.0	15.9	22.8	27.5	32.1
Saxifraga bronchials	W	9.5	14.0	15.9	23.7	27.7	31.3
	NW	8.3	11.3	15.7	22.8	27.7	31.4
Silene acaulis	W	8.5	13.2	15.5	23.0	25.5	30.0
	NW	8.2	11.1	15.6	22.2	25.5	30.1
Dryas octopetala	W	8.6	12.0	15.4	21.5	25.7	30.1
	NW	5.8	10.9	15.4	22.7	26.4	31.3

Appendix 16): Drying_out curves and stomatal apertures of detached transpiring organs of different species

App.(16.A): Eriogonum androsaceum (n=4).

	Weight (mg)
Fresh weight	095.2(15.3)
Saturated weight	157.7(18.2)
Weight after 10 min	140.2(18.1)
20	126.8(17.5)
30	112.9(17.0)
40	100.2(15.6)
50	096.6(15.2)
60	088.3(13.1)
70	082.7(12.7)
80	077.7(12.5)
90	073.4(11.4)
02 hr	065.5(11.2)
02.5	058.2(11.2)
03	050.3(10.8)
03.5	040.8(10.8)
04	040.2(10.6)
04.5	040.0(10.5)
05	030.8(10.5)
Oven dry weight	022.4(02.6)

App.(16.B): Potentilla uniflora. (n=5).

	Weight (mg)
Fresh weight	415.5(12.5)
Saturated weight	639.3(34.4)
Weight after 10 min	595.0(30.8)
20	499.1(24.3)
30	456.1(18.9)
40	426.4(15.3)
50	413.3(13.8)
60	403.9(13.4)
70	397.5(13.0)
80	391.8(12.7)
90	383.8(13.1)
02 hr	373.0(13.0)
02.5	363.4(12.9)
03	354.5(12.8)
03.5	344.8(12.7)
04	336.8(12.5)
04.5	328.9(12.7)
05	319.4(12.4)
Oven dry weight	135.0(04.8)

App.(16.C): Saxifraga caespitosa. (n=4).

	Weight (mg)	Stomatal aperture (um) Width	Length
Fresh weight	709.2(42.9)		
Saturated weight	892.7(58.5)	4.5(0.62)	11.8(1.00)
Weight after 10 min	875.1(57.8)		
20	855.6(57.2)	4.0(0.33)	11.3(0.88)
30	831.8(55.8)		
40	812.6(53.5)	2.8(0.83)	10.8(1.20)
50	803.5(51.7)		
60	772.6(49.6)	1.5(0.50)	09.3(0.88)
70	763.6(48.2)		
80	753.5(47.1)	0.8(0.25)	08.3(1.18)
90	751.0(46.8)	0.2(0.00)	01.0(0.13)
02 hr	742.7(46.2)	0.0	00.0
02.5	737.6(45.9)		
03	730.5(45.6)		
03.5	722.6(45.4)		
04	718.9(45.2)		
04.5	712.5(45.2)		
05	709.1(45.0)		
Oven dry weight	137.9(10.1)		

App.(16.D): Saxifraga bronchialis. (n=5)

	Weight (mg)	Stomatal aperture (um) Width	Length
Fresh weight	435.2(20.2)		
Saturated weight	476.6(22.4)	3.5(0.50)	10.8(0.95)
Weight after 10 min	458.1(21.5)		
20	443.8(20.8)	3.5(0.40)	10.5(0.40)
30	431.0(20.3)		
40	423.7(19.6)	2.0(0.63)	09.5(1.88)
50	420.6(19.2)		
60	418.6(19.1)		
70	416.9(18.9)	0.8(0.40)	04.2(1.10)
80	414.9(18.7)		
90	413.7(18.6)	0.4(0.20)	02.5(0.50)
02 hr	412.4(18.8)	0.2(0.10)	01.5(0.30)
02.5	410.4(19.0)	0.0	00.0
03	409.6(18.9)		
03.5	408.2(19.0)		
04	407.8(19.0)		
04.5	407.1(18.9)		
05	406.3(18.9)		
Oven dry weight	081.7(04.6)		

App.(16.E): Silene acaulis. (n=5).

	Weight (mg)	Stomatal aperture (um) Width	Length
Fresh weight	322.2(09.8)		
Saturated weight	371.1(10.6)	3.8(0.8)	11.5(1.2)
Weight after 10 min	355.4(10.5)		
20	343.2(10.3)	3.5(0.6)	11.3(1.0)
30	334.6(10.2)		
40	327.1(09.8)	3.3(1.0)	11.0(1.2)
50	321.5(10.0)		
60	315.5(09.6)		
70	310.4(09.7)	2.0(0.5)	06.4(0.8)
80	304.9(09.4)		
90	300.1(09.2)	0.3(0.1)	01.5(0.4)
02 hr	292.8(09.2)	0.1(0.0)	01.0(0.5)
02.5	281.5(09.4)	0.0	00.0
03	276.1(09.0)		
03.5	269.2(09.1)		
04	265.5(08.9)		
04.5	259.5(09.1)		
05	254.0(09.3)		
Oven dry weight	056.9(02.2)		

App.(16.F): Dryas octopetala. (n=5).

	Weight (mg)
Fresh weight	373.4(22.6)
Saturated weight	464.0(32.1)
Weight after 10 min	437.5(30.4)
20	401.1(28.0)
30	380.7(26.1)
40	364.4(24.8)
50	357.3(24.2)
60	352.2(24.3)
70	347.3(24.0)
80	343.4(24.0)
90	337.9(23.7)
02 hr	328.5(22.8)
02.5	319.8(22.7)
03	313.1(22.2)
03.5	306.1(21.9)
04	301.1(21.3)
04.5	294.3(20.8)
05	289.2(20.1)
Oven dry weight	128.6(11.0)